THE GASTROPOD GENUS THATCHERIA AND ITS RELATIONSHIPS

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ALAN JACK CHARIG



Pp. 255-297; Plate 47; 10 Text-figures

BULLETIN OF

THE BRITISH MUSEUM (NATURAL HISTORY) GEOLOGY Vol. 7 No. 9

LONDON : 1963

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), instituted in 1949, is issued in five series corresponding to the Departments of the Museum, and an Historical series.

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 7, No. 9 of the Geological (Palaeontological) series.

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Issued July 1963

Price Sixteen Shillings

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SYNOPSIS

The literature on the subject is reviewed with particular reference to the systematics of the genera concerned.

A Recent gastropod shell, Brit. Mus. (Nat. Hist.) no. 1960.154, is identified as the holotype of the type-species of *Thatcheria* (*T. mirabilis* from off Japan). The description is amplified.

The form of the posterior sinus in *Clinura* has been generally misunderstood. The protoconch, hitherto unknown in the genus, is described in the type-species and in one other. The protoconch of *Waitara liratula* is re-examined.

The systematics of the genera concerned are reconsidered. *Clinura* is restricted to a few species from the Neogene of Europe and of the Western Pacific. *Clinura, Waitara* and *Thatcheria* are closely related to each other but not to *Surculites*. Fourteen species in those three genera are reclassified into two genera, *Clinura* (mainly Miocene) and *Thatcheria* (Upper Miocene to Recent, mainly Pliocene); *Thatcheria* is confined to the Western Pacific. The two genera constitute a sub-family of the Turridae, the Thatcherinae, which has affinities with the Daphnellinae.

Thatcheria vitiensis sp. nov. is described and figured from one specimen of probable Lower Pliocene age from Fiji.

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I. INTRODUCTION

THE discovery of a new fossil gastropod which resembles *Thatcheria* and *Waitara* has led to a re-examination of this little-known group of genera. The conclusions reached have been based upon all the relevant literature and upon a few shell characters hitherto unknown or imperfectly understood.

Some of the earlier descriptions and illustrations of the gastropods in question were inadequate or misleading (especially with reference to the form of the posterior sinus and of the consequent growth-lines, the taxonomic significance of which had not then been appreciated). One drawing in particular, upon which some later workers relied for their knowledge of a type-species, is also quite different in that respect from the less accessible description and figures of the original author. The extreme scarcity of actual material obliged most later workers to rely very largely upon these earlier descriptions and figures, and misunderstandings therefore arose. Language difficulties appear to have exacerbated the situation. Finally, it is also evident that certain important works on the *Thatcheria-Waitara* group of gastropods were written in ignorance of the existence of some of the others. But this was sometimes unavoidable ; for example, two of the most important were written and published at about the same time during the Second World War, one in New Zealand and the other in the German-occupied Netherlands.

Thus, while the known members of the group are few in number, both as species and as individuals, their systematics are confused. Although only two named species (*Thatcheria mirabilis* and *T. gradata*) have been referred to the genus *Thatcheria* itself, those two species have already been placed by various authors in ten different prosobranch taxa of the genus-group (excluding synonyms). They have been considered, at least implicitly, as belonging to eight different prosobranch families, five of which possess alternative names. Indeed, one author alone (Wenz, 1943) has referred the two forms concerned and the closely related genus *Waitara* to three separate families. It has also been suggested that *T. mirabilis* is an opisthobranch, and elsewhere stated quite dogmatically that it is a "scalariform monstrosity". In all, in connexion with *T. mirabilis* and *T. gradata*, sixteen family names are involved.

However, it is now generally accepted that these molluscs are so closely related as to form a natural group. The group might be either a sub-family within the Turridae or, as has been suggested, a separate family with strong affinities therewith. The status and relationships of the group require careful consideration, and the systematics within the group are in need of revision.

II. HISTORY OF *THATCHERIA* AND OF THE VIEWS ON ITS RELATIONSHIPS

Thatcheria mirabilis gen. et sp. nov. was described and figured by Angas (1877: 529, pl. 54, figs. 1*a*, *b*). His material consisted of one fairly large pagodiform shell believed to be unique; it had been brought from Japan not long before by Mr. Charles Thatcher, and its occurrence could be localised no more accurately than "Seas of Japan". No indication was given as to where the shell was deposited.

Of its systematic position, Angas wrote : "Without a knowledge of the operculum, its exact generic position cannot be determined ; but at present I regard it as belonging to the subfamily Fusinae " (i.e. in the family then called Fusidae, now either called Fusinidae or regarded as part of the Fasciolariidae).

The next reference to the specimen is by G. B. Sowerby (1880 : 105, pl. 422, figs. 45, 46), who wrote that it "has been thought to exhibit, in the arched sinus of the outer lip above the angle, a peculiarity of generic value." He nevertheless referred the species to the genus *Pyrula*. (The "*Thesaurus Conchyliorum*" does not place genera in families, but the genus *Pyrula* Lamarck 1799, which should be replaced by the older synonym *Ficus* Röding 1798, is now referred to its own family Pyrulidae or Ficidae). Sowerby also considered Angas' type to be immature, and mentioned that it was "in the collection of Mrs. Deburch".

Tryon (1881: 98, 112, pl. 44, figs. 238, 239) retained Angas' genus *Thatcheria* and referred it to the sub-family Melongeninae or Melongeninae of the family Buccinidae; but his arrangement might indicate that he considered *Thatcheria* to be synonymous with the older genus *Hemifusus* Swainson. Further, he opined that Angas' specimen did not represent the normal form of the genus, for he wrote "That this shell is a scalariform monstrosity cannot be doubted". Later (1883:135, pl. 49, fig. 5) he gave an exact repetition of his earlier text.

Fischer (1884:623) reported Tryon as considering *Thatcheria* to be a scalariform monstrosity of "*Semifusus* Swainson em. 1840 (*Hemifusus*)." In fact, *Semifusus* Agassiz 1846 is an invalid emendation of *Hemifusus* Swainson 1840. Fischer placed this genus in the sub-family Melongeninae of the family Turbinellidae (sometimes called Xancidae or Vasidae); the sub-family in question is now generally regarded as a separate family, the Melongenidae.

Cossmann was at first (1889: 162) unable to agree with Tryon on this matter; the form of the sinus, as indicated by the growth-lines on the ramp, led him to believe that *Thatcheria* could well be a junior synonym of *Mayeria* Bellardi 1873. *Mayeria*, in any case, seemed to be close to "*Semifusus*", for Cossmann placed them both together (in the same family and sub-family as Fischer had done). Later, however (1901: 62, 93, 94), Cossmann decided that the canal of *Thatcheria* distinguished it from *Mayeria*, and that Tryon was correct after all in supposing *Thatcheria* to be but a monstrosity of "*Semifusus*".

Meanwhile Pilsbry (1895 : 28) had reverted to Tryon's classification and had listed *Thatcheria mirabilis* in the Buccinidae.

No further mention of *Thatcheria* has been discovered earlier than Tomlin's editorial notes (1919:66), in which he stated that the de Burgh Collection was offered for sale and that it included *Thatcheria mirabilis*, frequently considered to be a monstrosity of *Fusus*. (Presumably Tomlin intended this to refer to the genus *Fusinus* Rafinesque 1815 emend. pro *Fusus* Lamarck 1799, *non* Helbling 1779).

Yokoyama (1928: 338, pl. 66, figs. 3, 4) described and figured two specimens from the Pliocene of Japan as *Cochlioconus gradatus* gen. et sp. nov. The new genus was not explicitly referred to any family, but it was described as "*Conus*-like" and Yokoyama stated that "The presence of a deep sutural notch reminds us of the genus *Conus*." Pilsbry saw this paper and wrote to Yokoyama, drawing his attention to the similarity between *Cochlioconus* and *Thatcheria*. Yokoyama then stated in a subsequent paper (1930) that he regarded *Thatcheria* (*T. mirabilis*) and *Cochlioconus* (*C. gradatus*) as congeneric, though not conspecific, the Pliocene species being more *Conus*-like in appearance than the Recent form. He did not, however, change his views on the systematic position of the genus, for he wrote (p. 406) "I think I am right in placing it near *Conus*. This opinion seems to be also shared by Mr. Pilsbry as is evident from his communication." He also stated, probably wrongly, that Angas' specimen of *T. mirabilis* "may be the only one now existing [i.e., in a collection] in the whole world."

Thiele (1929: 320) considered *Thatcheria* to be a synonym of the sub-genus ("sectio") *Semifusus* sensu stricto, which he placed in the family Galeodidae. The proper family name is in fact Melongenidae, the name of the type-genus *Galeodes* being a junior homonym (Röding 1798 *non* Olivier 1791). Thiele, who was concerned only with Recent molluses, did not mention *Cochliocomus*.

S. Hirase (1934: 104, pl. 128B, fig. 3) figured a specimen of "*Thatcheria mirabilis* Angas (= Semifusus m.?)", which is appreciably longer and more slender than Angas' type. The illustration is of interest in that it showed, for the first time, that more than one individual of the species had been found.

This point was emphasised in 1937 at an Ordinary Meeting of the Malacological Society of London, at which Tomlin exhibited two shells of the species, both from Japan. Hopwood wrote in the *Proceedings* (1937:158) that "Tryon's dictum [that *Thatcheria* is a scalariform monstrosity] has been confuted recently by the discovery of several examples, but where it should be placed systematically is as great a problem as ever. Discussion elicited suggestions that it was a prosobranch to be placed in Turridae and that it was an opisthobranch allied to *Akera*." The suggestion that it was a turrid had not been made before.

The first recorded find of the soft parts of *Thatcheria* was made at about this time; Tomlin had obtained from a Japanese fisherman the anterior portion of a male animal, which was described and figured by Eales (1938). Unfortunately the specimen had lost the radula. Eales concluded, however (p. 16), that its characters "show that the specimen belongs to the Toxoglossa." A comparison of the creature with various members of the Turridae (e.g., *Turricula javana*) and of the Conidae (e.g., *Conus quercinus*) showed a very close resemblance to the former and none whatever to the latter; and an X-ray photograph of the shell of *T. mirabilis*, which "shows a typical columella similar to that of the Turrids, not resorbed as in the Cones", confirmed Eales' opinion (p. 17) that "As far as it is possible to judge *Thatcheria mirabilis* should be placed with the Turrids."

The next paper to mention *Thatcheria* was that of Powell (1942), in which he suggested a close affinity between *Thatcheria* and the fossil *Waitara*. At this point it is necessary to digress a little upon the latter genus.

All the species mentioned immediately below and referred to *Waitara* are from New Zealand. Marwick (1926: 324, pl. 74, fig. 9) had described a specimen from the Upper Miocene under the new specific name *waitaraensis*, referring it to the genus *Turricula*; but he also wrote (p. 326) that "the generic location of the Turridae described above is quite provisional. New genera seem to be required". Later (1931: 149) he erected the new genus *Waitara* upon this species, and referred thereto another new Miocene species, *W. generosa* (pl. 18, fig. 339). Powell (1942: 168) considered *W. generosa* to be of Lower Miocene age. Powell also described two more species of *Waitara* in the same work—*W. pagodula* (p. 168, pl. 14, fig. 7) from the Upper Miocene or Lower Pliocene and *W. liratula* (p. 169, pl. 14, fig. 8) from the Lower Pliocene—and mentioned yet another Lower Pliocene species (p. 168), represented by a single specimen too poorly preserved for description or illustration but said to be "somewhat similar [to *W. pagodula*] but narrower". The *Waitara liratula* material included the protoconch illustrated in his text-fig. B3 (p. 38). The paper gave a key to the four named species of *Waitara* (p. 168).

Powell's systematic conclusions were important. He wrote (p. 167) "It is possible that *Waitara* may yet prove to be identical with *Thatcheria* . . . and *Cochlioconus* . . . In any case all three are closely allied and represent a discordant Turrid-like group that cannot be satisfactorily placed in any of the nine sub-families adopted in this bulletin. . . . *Cochlioconus* is almost certainly a synonym [of *Thatcheria*], although its author made no reference to *Thatcheria*, but compared his genus with the Cones. Anyone acquainted with *Thatcheria* would scarcely have overlooked the need for some comparison." Evidently Powell did not know of Yokoyama's second paper on this subject ; nor, indeed, does he seem to have been aware of Eales' work. He sought to differentiate *Waitara* from *Thatcheria*, at least provisionally, because its sinus "although very similar to that of *Thatcheria*, does differ at its point of origin, in being narrowly concave before swinging forward, whereas the sinus in *Thatcheria* swings forward immediately." He also described the form of the sinus in all these genera as "deep Conid-like." Finally, after discussing the relationship of the genera in question to certain sub-families of the Turridae (the Daphnellinae and the Cochlespirinae) and to the Conidae, Powell came to the following conclusions (p. 168) :

"In order not to prejudice the status of the other Turrid subfamilies by forcing in such an aberrant group, it seems advisable to consider *Thatcheria* and its allies as representative of a new family, closely akin or parallel to the *Turridae*, for it seems to have arisen from the *Conidae*, but probably much later and independent of the early Conid-like Turrid divergent stock as represented by the *Conorbiinae*." He called this new family the Thatcheriidae; and, in the same work (p. 170), he wrote "The former [i.e. the Thatcheriidae] in having marked Conid affinity in respect to its sinus is indicated as a late Tertiary offshoot from the *Conidae*..."

Wenz (1943) evidently saw no connexion between *Thatcheria*, *Cochlioconus* and *Waitara*, for he placed all three in different families. He considered *Thatcheria* (p. 1215) to be a synonym of the sub-genus *Hemifusus* of the genus *Pugilina* Schumacher 1817, family Galeodidae. *Cochlioconus* (mis-spelt "*Cochliconus*" in the text on p. 1470 and in the index on p. 1604, though correct in the legend to fig. 4154) he regarded as a sub-genus of *Conus* Linnaeus 1758, family Clavatulinae, family Turridae; he wrongly cited *W. generosa* Marwick as the type-species, wrongly quoted its horizon as *Upper* Miocene and gave the stratigraphical range of the genus as Oligocene to Miocene, although no Oligocene species of *Waitara* has ever been

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recorded. (The Pliocene species of *Waitara* described by Powell (1942) were, of course, unknown to Wenz because of the Second World War.) The genus *Clinura* Bellardi 1875 (see below) was also included by Wenz (p. 1390, fig. 3928) in the Clavatulinae, as a sub-genus of *Surculites* Conrad 1865.

Beets (1943a: 296) described as *Surculites* (*Clinura*) bituminatus a new species of gastropod from the asphalt deposits of the island of Buton, off Celebes; the deposits were at that time believed to be of Upper Oligocene age. Like Wenz, Beets regarded *Clinura* as a sub-genus of *Surculites* and considered these forms to be turrids. In his description of S. (C.) bituminatus he placed *Cochlioconus* in the synonymy of *Clinura*; but, when doing so, he knew nothing of *Thatcheria*, for it was not until later that Yokoyama's second paper (1930) drew his attention towards that genus.

Perhaps the most important work of all on this group of gastropods was a second article by Beets (1943b). He suggested that Thatcheria (including, fide Yokovama, 1930, Cochlioconus), Clinuropsis Vincent 1913 (non Thiele "1931" [should be 1929]) and Nekewis Stewart "1926" [should be 1927] should all be regarded as junior synonyms of the sub-genus Clinura. In this paper Beets discussed a large number of species—of Clinura, of Clinuropsis, and of other genera such as Cryptoconus, Surculites, "Pseudotoma", "Surcula", "Pleurotoma" and "Turricula"—in order to ascertain whether they might properly be included in *Clinura*; and, since he considered their great variations in form (especially that of the posterior sinus) to fall within the range of the "für die so schwierigen Turridae ' normalen Variabilität ' ", his decision was usually affirmative. He concluded (p. 365): "Clinura ist jetzt mit Gewissheit bekannt aus dem Eocän bis Miocän der atlantischen [surely that should be " pazifischen "?] Küstenregionen Nordamerikas . . . , aus dem Montien bis Pliocän Europas und dem Oligocän des ostindischen Archipels; in Japan tritt sie erst ins Pliocän auf und lebt dort mit einer einzigen, extremen rezenten Art fort. Vielleicht (?) ist Clinura auch noch bekannt aus dem Eocän S.W. Afrikas und des Congos, höchstens mit zwei Arten."

At this point it may be useful to give a short account of *Clinura* and of its author. The genus was erected by Aloysius Bellardi (1875:20) in a paper written entirely in Latin ; although "A. Bellardi " and "L. Bellardi " (Luigi) are sometimes listed separately in bibliographies (e.g., Wenz, 1944:1513), there are several reasons which make it seem certain that "Aloysius" was merely a latinisation of "Luigi" and not the name of another author. First, both "Aloysius" and Luigi were Professors of Natural History, living at the same time in the same country and writing on the same subject ; indeed, not only " Aloysius " but also Luigi published works concerned with Clinura, including the one mentioned below in which Luigi quoted verbatim (but without acknowledgment) the generic diagnosis given by "Aloysius" and then designated a type-species. Secondly, both "Aloysius" and Luigi published in the Bullettino della Società Malacologica Italiana; and authors of works in that journal were generally members of the society in question, yet only Luigi's name is to be found in the list of members for 1875. Thirdly, "Aloysius" (unlike Luigi) published nothing except this one paper. Fourthly, neither "Aloysius" nor Luigi, when referring to names proposed by a Bellardi or to previous publications by a Bellardi, was in the habit of distinguishing himself from the other

by the use of an initial. Fifthly, a paper in French by "Louis" Bellardi (1841) is clearly the work of Luigi; it is therefore evident that Luigi was in the habit of altering his Christian name to conform with the style of the language in use. Finally, an obituary of Bellardi by his fellow malacologist Sacco (1889) gives a list of the "Publications scientifiques de M. Louis Bellardi"; this includes all the works of "Aloysius", Luigi and "Louis", and thus provides conclusive proof of their identity.

The 1875 paper designated no type-species for *Clinura* but assigned two species to the new genus, *C. calliope* (Brocchi, 1814:436, pl. 9, figs. 15*a*, *b*) [*Murex*] and *C. elegantissima* (Foresti, 1868:598, pl. 2, figs. 10–13) [*Pleurotoma*]; Bellardi placed *Clinura* in his new sub-family Pseudotominae, family Pleurotomidae. A far more complete account of the genus, published a few years later in Italian by Luigi Bellardi (1877:204-209), included five species therein; *Clinura calliope*, from the Upper Miocene of Italy, was clearly designated as the type (p. 204). Other fossil species were subsequently referred to the genus, at first only from the Neogene of Europe, e.g., R. Hörnes & Auinger, 1891:362; Friedberg, 1912:210); later, however, species from rocks as old as the Eocene and as far away as California and Celebes were also placed in *Clinura* (e.g., Grant & Gale, 1931: 494; Beets, 1943*a*, 1943*b*, as indicated above).

Meanwhile two Recent deep-sea gastropod species had also been referred to Clinura, C. monochorda Dall (1908: 292, pl. 13, fig. 1) and C. peruviana Dall (1908: 293, pl. 13, fig. 2). Since these are the only Recent species ever referred to the genus, they are also the only species mentioned by Thiele (1929: 371), whose work did not deal with fossil forms. Thiele wrote of Dall's species, however, that "doch dürften sie mit dieser [Clinura] kaum verwandt sein", without giving any reason for this statement, and he proposed that these two species should constitute a new section Clinuropsis of the genus Pleurotomella Verrill 1873, with P. (C.) monochorda (Dall 1908) as the type-species. But, by the time he wrote his "Nachträge und Berichtigungen" to the same work, published in 1934, Thiele had learnt that the name Clinuropsis had already been used by Vincent in 1913; he therefore proposed (p. 1002) the new name Anticlinura to replace it.

Wenz (1943:1460) treated the supposed Recent species of *Clinura* exactly as Thiele had done. Beets (1943b:364) also agreed with Thiele (1929) in the matter, Dall's species being two of the few which he chose to exclude from the genus *Clinura*; unlike Thiele, he gave reasons (such as the presence of lattice-like sculpture on Dall's species) for so doing. Further, Beets appears to have noted Vincent's preoccupation of the name *Clinuropsis* but not Thiele's subsequent correction and proposal of *Anticlinura* nom. nov. to replace *Clinuropsis* Thiele; for he himself, with the same intention, proposed *Clinuromella* nom. nov. Thus *Clinuromella* Beets 1943b is an objective junior synonym of *Anticlinura* Thiele 1934, both being new names for *Clinuropsis* Thiele 1929 (non Vincent 1913). In conclusion, it would seem that Dall's two species should continue to be placed under the sub-generic name *Anticlinura* (of which monochorda is the type-species) in the genus *Pleurotomella*.

No author has ever disputed the position of *Clinura* in the Turridae (Pleurotomidae). Cossmann (1896) and Friedberg (1912) both regarded the taxon as a sub-

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genus of *Surcula* H. & A. Adams 1853; but Grant & Gale (1931) considered it to be a sub-genus of *Surculites*, in which opinion, as recorded above, they were followed by Wenz (1943) and Beets (1943*a*; 1943*b*). Wrigley (1939), however, while not denying the turrid (or at least toxoglossan) nature of *Clinura*, believed that *Surculites* was not a turrid and therefore not related to *Clinura*.

Thus the connexion of *Thatcheria* with *Clinura* was suggested and firmly established in 1943. The rest of this historical account will deal also with papers referring to *Clinura*, even though they make no mention of *Thatcheria*.

Though complete in most respects, Beets' paper (1943b) had not considered *Waitara*. Powell's bulletin on the Turridae, published in New Zealand in 1942, drew attention to the relationship between *Waitara* and *Thatcheria*, but had not been seen by Beets working in that same year in the German-occupied Netherlands; nor could he have seen Wenz's treatise (1943) which placed *Waitara* immediately next to *Clinura*. In 1949, however, Beets obtained access to Powell's bulletin; and in 1951 he published yet another paper, one part of which was concerned with "*Waitara* and its relationships to *Surculites-Clinura-Thatcheria*." The main object of this work was to establish *Waitara* as part of "the species group *Clinura* . . . (taken in a broad sense) "; the three taxa *Clinura*, *Waitara* and *Thatcheria*, hitherto related only as three different pairs by three different authors, were to be brought together. Beets recognised, however, that Wenz's conclusions regarding the taxonomic proximity of *Waitara* and *Clinura* had been based entirely on Marwick's original Miocene species of the former genus, while the affinities of that genus to *Thatcheria* depended more on the characters of the younger species described by Powell (1942).

One noteworthy point from Beets' 1951 paper is that, whereas he had earlier (1943b) considered *Thatcheria* to be a synonym of the sub-genus *Clinura*, he now regarded *Clinura*, *Waitara* and *Thatcheria* as three separate (but closely related) sub-genera, still in the genus *Surculites*. He gave no reason for this change. Incidentally, this work of Beets contains three minor errors. First, he stated (p. 14) that *Turricula waitaraensis* Marwick became the type-species of *Waitara* by Powell's subsequent designation in 1942; it was, in fact, the type-species by Marwick's original designation (1931). Secondly, he appeared to claim (p. 15) that he himself was the first to refer *Thatcheria* to the Turridae (1942b, cited in the present work as 1943b); he was, of course, preceded in this by Eales (1938). Thirdly, he quoted Powell (p. 16) as describing the posterior sinus of *Waitara* as "first narrowly convex"; that should read "concave".

Beets (1951) also gives a small, semi-schematical figure (pl. 1, fig. 6) of "*Thatcheria* spec. nov.; a portion of a specimen from the Pliocene of East-Borneo". The fragment was mentioned only briefly in the text (p. 16) and has not yet been described. It appears to consist of two whorls from a pagodiform spire which must indeed have been remarkably like that of *T. mirabilis*, with a similar type of sinuosity in the growth-lines on the ramp.

The asphalt deposits of Buton (which, according to Beets (1943a; 1943b), contained two species of *Clinura*) were supposed to be of Upper Oligocene age. In 1953, however, Beets showed (p. 239) that the age of the molluscan fauna was most likely Mio-Pliocene; there is no evidence to support the suggestion that the molluscs might be a mixture derived from different stratigraphical horizons, but the possibility cannot be entirely excluded. He also reported Reinhold as concluding that the diatoms in the deposits indicate a probable Upper Miocene age.

S. Hirase's posthumous handbook of Japanese shells (1951), which was in effect his catalogue of 1934 revised and enlarged by Taki, reproduced the figure of *Thatcheria mirabilis* which had appeared in the earlier work (pl. 128B, fig. 3, in both). The later work, however, no longer suggests that *Thatcheria* might be a synonym of "Semifusus"; and the second edition (1954) is provided with a systematic index to the plates which, on p. 88, classifies *Thatcheria* as a genus of the Turridae.

Thatcheria was also listed among the Turridae by Kuroda & Habe (1952:10). On p. 90 of the same work they indicated that the geographical range of *T. mirabilis* was off the Pacific coast of Japan, between 33° and 35° of latitude.

Hatai & Nisiyama (1952:191) listed Yokoyama's two syntypes of *Cochlioconus* gradatus with full details of locality and horizon; the latter was given as Takajo Formation, believed to be of Lower Pliocene age. It was noted that both specimens were in the collections of the Geological Institute of the Faculty of Science of Tokyo University. The specimen illustrated in Yokoyama's fig. 3 (1928, pl. 66) was designated as lectotype ("holotype") by these authors, who evidently regarded *C. gradatus* as a junior synonym of *Thatcheria mirabilis*.

Kuroda & Habe (1954:80) published important new information on *Thatcheria mirabilis*; this was obtained from three individuals of different ages, each with soft parts. They were able to describe and figure the radula (text-fig. 2) and the protoconch (text-fig. I, showing also the early nepionic whorls); the operculum was reported lost in all the specimens. The peculiar shape of the radula and the obliquely reticulated sculpture of the protoconch led them to suggest that *Thatcheria* was a member of, or had a close affinity with, the Daphnellinae. Unfortunately they had misinterpreted both Eales' and Powell's papers. First, they thought that Eales' observation, "No traces of proboscis or radula are present", indicated the natural lack of a radula in the species ; but, in fact, the lack of a radula was clearly accidental in the specimen which constituted the whole of Eales' material, "the body being torn away immediately posterior to the mouth tube." Secondly, they believed that Powell had established the family Thatcheriidae to include, not only *Thatcheria mirabilis* and some fossil species, but also some other, related Recent groups (but no others are known); and further, that Powell had done this because of the "nature of its radula quite rudimentary" in *Thatcheria* (also unknown at that time).

Habe (1955) devoted two short articles to "*Thatcheria mirabilis* Angas (Turridae)". The first is in English; it consists only of a direct quotation of Angas' description, reproductions of the figures of the early whorls and the radula (from Kuroda & Habe 1954), references to the works of Angas, Eales, Powell, and Kuroda & Habe, and the comment "This strange species seems better to locate under the sub-family Daphnellinae in having the reticulated protoconch and the dart shaped radula." The other article is in Japanese but is not the same; it reproduces the illustrations to Angas' paper, cites the dimensions of three new specimens of *T. mirabilis* and mentions the fossil *Cochlioconus*.

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Kira (1955 : 71, pl. 35, fig. 19) also placed Thatcheria mirabilis in the Turridae.

Rossi Ronchetti (1951-56) included *Murex calliope*, the type-species of *Clinura* (see p. 263), among the species dealt with in her review of Brocchi's types; she selected, figured and carefully described a neotype (1955: 305, fig. 163) because Brocchi's holotype was no longer preserved. The species appears, however, under the name *Pleurotomella* (*Clinuropsis*) calliope, presumably for the following reasons:

The introduction to Rossi Ronchetti's review stated (1951:11) that the revision of the generic names would be based partly upon the works of Wenz (1938–44) and Schilder (1932), partly upon the works of Thiele (1929–31, 1934–35). Schilder, of course, dealt only with Cypraeacea. In this particular instance Rossi Ronchetti could not have used Wenz (or Thiele's "Nachträge und Berichtigungen") as the basis for her classification ; had she done so, she would then have known—as she clearly did not know—that Thiele had later proposed Anticlinura as a new name to replace his own Clinuropsis. It therefore appears likely that she based her classification only upon Thiele's main work. Noting that Dall's species of Clinura, the only supposed representatives of that genus mentioned by Thiele, had been transferred by the latter author to Pleurotomella (sectio Clinuropsis), Rossi Ronchetti did the same with Clinura calliope—probably without considering the possibility that Dall's species had no real connexion with Clinura.

Although other authors may not agree that calliope Brocchi and monochorda Dall are co-sub-generic, or even congeneric, Rossi Ronchetti is nevertheless entitled to her opinion that they are. In that case she was correct in using for both species the oldest generic name available—*Pleurotomella* Verrill 1873. But, for the subgenus, she should then have used the oldest generic name previously applied to any included species—and this was *Clinura* Bellardi 1875, not *Clinuropsis* Thiele 1929 (which, in any case, was preoccupied). Moreover, according to Grant & Gale (1931: 510), *Pleurotomella* Verrill 1873 (type-species *P. packardii* Verrill 1873) is a subjective junior synonym of *Pleurotomoides* Bronn 1831 (type-species *Defrancia pagoda* Millet 1826).

With respect to *Clinura*, Eames (1957:51) adopted the classification of Grant & Gale, Wenz, and Beets, in which *Clinura* appears as a sub-genus of *Surculites* in the Turridae. But he referred the Eocene species *Surcula ingens* (Mayer-Eymar 1896) [*Pleurotoma*] to *Clinura*, although Beets (1943b:363) had clearly expressed the opinion that it was not related thereto and represented an altogether different group.

The Fiji Geological Survey Department, in its Annual Report for the year 1958 (1959), mentioned on p. 15 the collection of an unusual fossil shell from the island of Vanua Levu, identified by the present writer as a new species of *Thatcheria*. The Report also quoted his observation (in litt.) " . . . as far as I am aware, the genus has never been recorded as a fossil."

Several gastropod species represented in the collections of the Institut Royal des Sciences Naturelles de Belgique were listed by Glibert (1960:25) under the generic name *Clinura*. They are all from the Tortonian or Plaisancian of Italy or the Vienna Basin. Glibert classified *Clinura* as a genus of the sub-family Cochlespirinae (family Turridae).

TABLE I.—SUMMARY OF VIEWS ON SYSTEMATIC POSITION OF THATCHERIA

(i.e., of the only two named species hitherto referred to that genus)

Author Sp.	Sub-genus	Genus	Sub-family	Family
Sowerby, 1880 . m .	_	Pyrula (juvenile)	·	[Pyrulidae
T		(= Ficus) Thatcheria, a	. Melongeninae,	(= Ficidae $)]$
Tryon, 1881, 1883 . m .		scalariform	Melongeniinae,	
		monstrosity listed		> Buccinidae
		under Hemifusus		
Pilsbry, 1895 . m .		Thatcheria		J
Thiele, 1929 m .		Semifusus		Galeodidae
Wenz, 1943 m .	(= Hemifusus s.s.) Hemifusus	(= Hemijusus) Pugilina		(= Melongen
Pchelintsev & m		Hemifusus		dae)
Korobkov, 1960				
Fischer, 1884		A scalariform		
Cossmann, 1901 m		monstrosity of		
			> Melongeninae	. Turbinellidae
C		(=Hemifusus) Mayeria		
Cossmann, 1889 . <i>m</i> . Angas, 1877 <i>m</i> .	•	Thatcheria	. Fusinae	
Aligas, 1077	•	1 ///////////	(= Fusi-	
			ninae)	I ≻[Fusidae
Tomlin, 1919 . m		A monstrosity of		(= Fusinidae
		Fusus	(= Fusi-	
1		(=Fusinus)	ninae)]	. ? Turridae
Hopwood, 1937 . m	•	Thatcheria		. ? Turridae
Eales, 1938 . Kuroda & Habe, 1952				
Hirase & Taki, 1954		Thatcheria		
Kira, 1955 .			}	. Turridae
	. Clinura .	Surculites		
		Surculites		
		Surculites	Deshaellinge	[Turnida a]
Kuroda & Habe, . m	• •	Thatcheria	. Daphnellinae	. [Iumdae]
1954 Habe, 1955 m g		Thatcheria	. Daphnellinae	. Turridae
Powell 1042		Thatcheria	-	. Thatcheriidae
MacNeil, 1960 mg	• •		•	. Inatchendad
Yokoyama, 1928 . g	• •	Cochlioconus	}	. [Conidae]
Yokoyama, 1930 . m g		Thatcheria)	
Wenz, 1943 . Pchelintsev & g	. Cochliconus .	Conus		. Conidae
Korobkov, 1960	(= Cochlioconus)	00,000		
Hopwood, 1937 . m		Thatcheria		. ? [Akeridae]
1				
Charig, 1963 m g		Thatcheria	. Thatcheriinae	. Lurridae

Note:

m indicates application to mirabilis Angas.

g indicates application to gradata Yokoyama.

Square brackets [] denote implicit references.

Where an author has used a junior synonym or homonym, or family name derived therefrom, the nam considered here to be correct is also given—in parentheses.

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The Osnovy Paleontologii (1960), edited by Pchelintsev & Korobkov, adopts a very conservative arrangement which seems to be based on that of Wenz; the important works of Eales, Powell, Beets, and Kuroda & Habe are all ignored. *Thatcheria* (p. 222) is given as a synonym of the genus *Hemifusus*, family Galeodidae; *Cochlicoconus* (p. 241), again mis-spelt "*Cochliconus*", appears as a sub-genus of *Conus*, family Conidae; *Waitara* (p. 240) is cited as a genus *incertae sedis* in the Pleurotomidae; and, in that same family, *Clinura* (p. 239) is still considered to be a sub-genus of *Surcula*.

MacNeil (1960: 120, pl. 15, figs. 11, 12) described two shells from the Neogene of Okinawa, now in the United States National Museum, as Thatcheria cf. T. gradata (Yokovama); he retained Powell's family Thatcheriidae for the genus. The figured specimen was from the Pliocene; the other was from rocks which might be a little older, perhaps of either [Lower] Pliocene or [Upper] Miocene age. Both were compared with T. gradata rather than with T. mirabilis because of their plane to slightly concave ramp (the ramp in T. mirabilis is "definitely depressed with the periphery slightly upturned "), the coarser sculpture, the lack of crowded spirals just below the periphery, and (presumably) the less pagodiform spire. The excellent preservation of the Okinawan specimen figured by MacNeil, with the sculpture preserved nearly to the protoconch stage, shows that "The early sculpture is strongly turrid, the periphery being ornamented with well defined blunt denticulations, about 9 or 10 visible from an angle, and the denticulations themselves are crossed by fine spiral lines"; in this respect comparison with Yokoyama's material is impossible, for the early whorls are not preserved in either of the Japanese specimens. Nor, for that matter, are they preserved in MacNeil's other Okinawan (possibly Miocene) specimen.

MacNeil also expressed some slight doubt as to whether the young shell figured by Kuroda [& Habe] (1954) was really a *Thatcheria*, pointing out that the first nepionic whorl is quite different from that of the Okinawan form. The figured specimen from Okinawa, however, lacks more of the apex than is represented by the whole of Kuroda & Habe's figure, and therefore a proper comparison cannot be made.

III. NOTES ON THATCHERIA MIRABILIS ANGAS

Identification of the holotype

It was suspected that the holotype of the species might be a shell in the collection of the Department of Zoology of the British Museum (Natural History), recently registered under the number 1960.154. The only available information pertaining to this specimen is that it formed part of the de Burgh Collection.

As mentioned above (p. 258), Angas gave no indication as to where his unique shell was deposited. But Sowerby wrote that it was "in the collection of Mrs. Deburch"; and a copy of Angas' original paper, now in the possession of Mr. S. P. Dance, bears the annotation "de Burgh Coll." in Fulton's handwriting. Finally, as also mentioned above, the de Burgh Collection was offered for sale in 1919 and included material of T. mirabilis. Although it was not stated explicitly that there was only one specimen, there is nothing to suggest that there was more than one; indeed, it was not until the nineteen-thirties that it became apparent that T. mirabilis was not just a unique monstrosity.

The British Museum specimen referred to has therefore been compared with Angas' description and illustrations. Its dimensions and individual peculiarities, especially the form of the mended break in the outer lip, show that, while the drawings (which bear the indication "G. Sowerby lith.") are not wholly accurate, the common peculiarities are so many that they cannot be merely fortuitous.

It may therefore be presumed that the B.M. specimen, registered number 1960. 154, is the holotype of *Thatcheria mirabilis* Angas.

Additional material in the British Museum

(1) The incomplete soft parts described by Eales (1938) (B.M. regd. no. 1937–12– 16.1). This specimen was obtained at Kii, Japan, and was presented to the Museum by Tomlin in 1937. The shell is missing, but it must be presumed that one was originally associated with these soft parts, for the latter could not otherwise have been identified; it may have been one of the two exhibited by Tomlin in 1937 at a meeting of the Malacological Society of London. (Tomlin's collection, lodged in the National Museum of Wales, Cardiff, includes two uncatalogued shells of *Thatcheria mirabilis* from Kii, and it seems likely that these are the same two.) Dr. Eales has no information on the subject.

(2) The shell of which an X-ray photograph was given in Eales' (1938) paper. This photograph was of "a specimen in Mr. Winckworth's collection". Winckworth's entire collection was later bought by the British Museum; the shell shown in the photograph may therefore be in the Museum's possession, but it cannot be found at present.

(3) Another shell (B.M. regd. no. 1937–7–9.40). This specimen is considerably smaller than the holotype (length 76 mm. as against 87 mm.). It too was obtained at Kii, Japan, and was bought from H. C. Fulton in 1937. It is certainly not the X-rayed specimen.

Supplementary description

Angas (1877) described *Thatcheria mirabilis* as having an "outer lip with a broad excavated sinus extending from its juncture with the body-whorl to the extremity of the last keel"; he gave no more precise indication of its form. His fig. 1*a* of the shell in apical view shows the margin of the posterior sinus (and all the collabral growth-lines parallel thereto) intersecting the edge of the preceding whorl more or less at right angles; as the margin passes outwards from that point it at once curves smoothly forward and then runs obliquely to meet the carina at an acute angle. His fig. 1*b* of the same shell in apertural view gives no more information on this matter.

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It is nevertheless obvious that, since each whorl is much wider at the carina than at the abapical suture, it will hide the inner part of the ramp of the following whorl when viewed from the direction of the apex; thus, in Angas' figure, the line which seems to terminate the margin of the sinus at its inner end is the carina of the preceding whorl. The margin of the sinus must in fact pass further adaxially beneath the carina to meet the (hidden) adapical suture. But what is the precise form of this inner part of the sinus margin?

Except for one drawing by Beets (1943b, referred to below), the work of subsequent authors has done nothing to make known the form of the posterior sinus in *Thatcheria mirabilis*; sometimes, indeed, the form of the sinus has been completely misunderstood. The holotype will therefore be briefly re-described, with particular reference to that feature.

The form of the sinus is clearly shown in Plate 47, fig. 3. The margin of the sinus does not pass perpendicularly outwards from its point of origin on the adapical suture, but extends obliquely outwards and backwards for a short distance; as it does so it curves right round until it is running obliquely forwards to meet the carina at an acute angle. The outer limb of this arch is much longer than the inner, so that any given growth-line meets the carina at a point which is much further forward than its point of origin, and the vertex or base of the sinus lies much nearer to the suture than to the carina—at about a quarter of the distance across the ramp. This type of sinus may be described as deep and juxtasutural, its depth being largely due to the forward extension of the outer lip.

Powell (1942: 167) was entirely misled by Angas' figure. He wrote that "*That-cheria* has . . . a very deep sutural sinus"; but, as mentioned above, he noted that *Thatcheria* seemed to differ from *Waitara* in that its sinus swung forward immediately from its point of origin.

Beets, on the other hand, seemed to understand the true nature of this sinus. In his drawing of T. mirabilis in apical view (1943b, pl. 36, fig. 2) the position of the suture, hidden by the projecting carina of the preceding whorl, is marked with a broken line : also marked are the whole of the margin of the sinus and of one growthline, rightly showing the hidden parts next to the suture passing backwards in an However, he paradoxically wrote (p. 361): "Der Sinus der Aussenlippe ist arc. vollkommen vergleichbar jenem der (anderen) Clinura-Arten ". Now this is true. But, as shown below, his conception of the form of the posterior sinus in Clinura was itself completely wrong; it was based on the misleading illustrations of other authors, so that he believed the sinus to be quite shallow. Further, he cited (Beets, 1951: 16) Powell's observations on the Thatcheria sinus, yet at the same time was puzzled by the apparent fact that the sinuses of Cochlioconus and Waitara, while similar to each other, differed from that of Thatcheria in that they were first narrowly concave.

The superficial ornament of the shell is another feature of T. *mirabilis* that has not been adequately described. Angas (1877) wrote of his holotype : "above the keels finely arcuately striate [i.e. with collabral growth-lines parallel to the margin of the posterior sinus], below irregularly more or less crenately concentrically ridged ". Beets (1943b: 361) included this description of the superficial ornament of T. *mirabilis* : " der Kiel ist glatt, auch der obere Windungsabschnitt ; vor der Kante sind die Umgänge wieder fein spiralig gefurcht."

There are, in fact, three distinct categories of superficial ornament. These are spiral ornament, running in the direction of growth of the helicocone; transverse ornament, running across (more or less) the direction of growth of the helicocone; and collabral ornament (growth-lines), parallel to the outer lip throughout the length of the latter. Transverse ornament, of course, is usually collabral, but is not necessarily so (Cox, 1955: 198).

In *Thatcheria mirabilis* there are indeed many distinct spiral furrows on the outer face, often arranged in pairs (Pl. 47, fig. 1). On the lower part of the outer face of the last whorl, within the inner lip, the furrows are soon obliterated by the forward growth of the edge of the mantle; thus each spiral furrow, if traced backwards and inwards for a few millimetres beyond the inner lip, disappears beneath a shining white layer of callus. The carina of the shell is smooth. Very weak spiral striations are present on the ramp, except on its innermost part next to the adapical suture. Transverse ornament is entirely lacking in *T. mirabilis*.

As for collabral lines, the form of the outer lip which produces them is simple and slightly convex between the anterior canal and the carina. On the ramp the outer lip delimits the posterior sinus, of which the form has already been described.

A final point to mention is that consideration of the length of all the nine measured shells of *T. mirabilis* recorded in the literature and in this present work leads to the conclusion that the holotype is an adult shell of average size. The measured lengths are 18 mm., 33 mm., 76 mm., 77 mm., 87 mm. (holotype), 89 mm., 94 mm., 97 mm. and 98.5 mm. Three other shells have been mentioned but without measurements; they are the third specimen of Kuroda & Habe (1954), which is presumed not to be the same as any of the three referred to by Habe (1955), and Tomlin's two shells in the National Museum of Wales. Thus, in all, twelve shells have been mentioned hitherto. There is at least one more shell in a private collection in England, there are probably several in the United States, and it is likely that there are further specimens in Japan and elsewhere. Indeed, *Thatcheria mirabilis*, once thought to be a unique monstrosity, is no longer even a great rarity.

IV. NOTES ON CLINURA

Material studied

The British Museum collections contain two well preserved specimens of *Clinura*; one of these belongs to the type-species C. calliope. The determinations were verified by detailed comparisons with the descriptions and figures of the original authors. Particulars of the specimens are as follows:

(1) Clinura calliope (Brocchi 1814) [Murex]. Brit. Mus. (Nat. Hist.) regd. no. G. 79439.

From the Plaisancian (Lower Pliocene) of Biot, near Antibes, Alpes Maritimes, France.

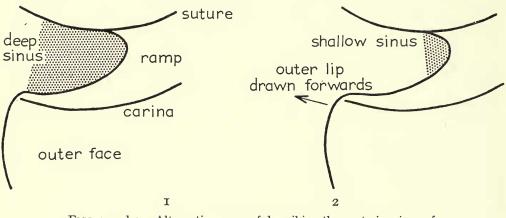
(2) Clinura trochlearis (M. Hörnes 1854) [Pleurotoma]. Brit. Mus. (Nat. Hist.) regd. no. GG. 2185. (This specimen was formerly in the Wrigley Collection.)

From the Zweite Mediterran-Stufe (Middle or Upper Miocene) of Walbersdorf, Burgenland, Austria.

This material was studied in order to ascertain the generic characters of *Clinura* rather than the specific characters of *C. calliope* or *C. trochlearis*. Since the former is the type-species, the latter was considered only in so far as it afforded additional evidence of those generic characters.

Posterior sinus

It is evident from Plate 47 that the posterior sinus of *Clinura calliope* (fig. 11) was exactly like that of *Thatcheria mirabilis* (fig. 3). But, just as in *T. mirabilis*, the form of the posterior sinus is not so readily apparent from the descriptions and has often been misunderstood—though in an entirely different way. In these fossil



FIGS. I and 2.—Alternative ways of describing the posterior sinus of *Clinura* and *Thatcheria*.

gastropods the outer lip with its sinus is usually broken away, and the form of the sinus must therefore be inferred from the form of the collabral growth-lines. Some of the earlier figures (and hence later ones copied from them) either did not show the growth-lines or else depicted them inaccurately; and it is unfortunate that later workers have sometimes ignored descriptions in foreign languages. Finally, the posterior sinus of *Clinura* has been variously described as "deep" or "shallow", even by the same author; this point requires explanation.

Confusion has probably arisen over the depth of the posterior sinus for the following reason. Some workers (including the present writer) define the posterior sinus as including the whole of the notch between the outer lip and the suture (Text-fig. 1). Others, however, have considered it to end anteriorly (with respect to the direction of growth of the helicocone) at the level of the junction of its margin with the suture (Text-fig. 2); in which case the sinus of *Clinura* must be regarded as shallow, but it is then necessary to mention that there is also a well developed forward extension of the outer lip.

The original author (Brocchi, 1814, pl. 9) gave two figures of Murex calliope which

were repeated in the later edition of his work (1843). His fig. 15a, in apertural view, shows nothing of the growth-lines on the ramp; but fig. 15b, in abapertural view, shows them fairly well. All that Brocchi wrote in this connexion (p. 436) was " \ldots si osservano alcune finissime rugosità obblique ed arcuate che sono le tracce dell'antico margine di quella sinuosità, che hanno tutte le pleurotome nel labbro destro, e ch'è il carattere del genere."

Bellardi (1847, pl. 1, fig. 9) depicted *Pleurotoma calliope* with strongly curved growth-lines in which both limbs of the arch appeared to be of about the same length; that is, the sinus would have been deep but symmetrical.

The same author (1875:20), proposing the new genus *Clinura*, gave only a generic diagnosis in Latin. This included two phrases which he later reproduced more grammatically (Bellardi, 1877:204) as "Sinus posticus labri sinistri valde profundus, arcuatus; labrum sinistrum antice valde productum, aliforme". But he also wrote on p. 204: "I caratteri principali di questo genere sono [inter alia]:

3° labbro sinistro sinuoso posteriormente ;

4° seno molto largo e poco profondo, foggiato ad arco, il quale parte direttamente dalla sutura posteriore ;

5° labbro sinistro protratto a guisa di ala ".

It is not easy to reconcile "sinus . . . valde profundus" with "seno . . . poco profondo "! Incidentally, it should be noted that the outer lip is the "labbro destro" of Brocchi but the "labbro sinistro" of Bellardi. In Bellardi's figure (1877, pl. 7, fig. 1) the little that can be seen of the growth-lines makes the sinus appear shallow.

Cossmann (1896:74) described the sinus of *Clinura* as "largement arrondi en quart de cercle incomplètement fermé et aboutissant presque perpendiculairement à la suture". His pl. 5, fig. 19 shows nothing whatever of the growth-lines.

It is evident that Grant & Gale (1931:494) based their idea of the form of the sinus in *Clinura* upon these works of Bellardi (1877) and Cossmann (1896), for they referred specifically to the figures of *C. calliope* therein. Thus they were led to write of the genus "posterior notch very wide and shallow, rounded". They also transferred to *Clinura* certain American species which, in fact, differ widely from *Clinura* in the form of their sinus.

Of modern authors, only Wrigley (1939: 283) seems to have been aware of the true form of the posterior sinus in *Clinura*; for he wrote of that genus, "the growth lines sweep back over the rear slope four or five times as far as those of *Surculites*". This character was not illustrated in his paper. Wrigley was wrong, however, in stating that *Nekewis io* (Gabb), from the Eocene of California, was much like *Clinura*; for Stewart's figure of that species (1927, pl. 30, fig. II) shows a fairly shallow, symmetrical sinus.

Beets (1943b: 359) cited the figures of Brocchi, Bellardi and Cossmann mentioned above, and then wrote: "Wie die Aussenlippe vor der Kante verläuft, ist nicht aus Bellardi's Abbildung abzulesen, wohl aber aus den anderen zitierten Figuren." His semi-diagrammatical drawing (1943b, pl. 36, fig. 8, pl. 37, fig. 23; 1951, pl. 1,fig. 3) is nevertheless based upon Bellardi's figure, to which has been added a growthline evidently consequent upon a very shallow sinus. Thus Beets too had been misled.

Rossi Ronchetti (1955: 306) was not informative on this point. She wrote of "*Pleurotomella*" *calliope* that "la maggior parte della superficie [della porzione posteriore . . . è] percorsa solo da strie di accrescimento alquanto arcuate." Her fig. 163 shows but the faintest trace of growth-lines, and then only the part nearest to the adapical suture.

As for *Clinura trochlearis*, examination of the material in the British Museum shows that its posterior sinus is just like that of *C. calliope*. Indeed, the form of the sinus in *C. trochlearis* was depicted very clearly by M. Hörnes in the figures to his original description (1854:363, pl. 39, figs. 14a, b, 15a, b) [*Pleurotoma*]; it has never been subject to misunderstanding.

Protoconch

No protoconch has yet been described in any species of *Clinura*; it may be that the apex of the shell was missing in all the material available to those working on the genus. But the two specimens in the British Museum, of which details have been given above, both possess a protoconch.

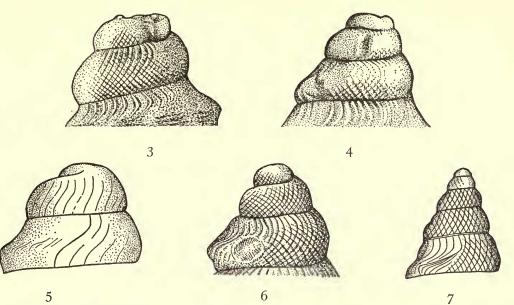
The protoconch of *C. calliope* (Pl. 47, fig. 12; Text-fig. 3) is well preserved, though probably incomplete above; two whorls remain. It is entirely covered with very distinct oblique cancellation, each thread being slightly concave towards the anterior side.

The protoconch of *C. trochlearis* (Text-fig. 4), of which two and a half whorls are preserved, is rather abraded. The upper and lower parts of each whorl are obliquely cancellate, just like the protoconch of the type-species, but the central, thickest part is worn smooth in places.

Transverse sculpture

The presence of transverse sculpture is well known in *Clinura calliope*. It consists of prominent tubercles on the carina; according to Rossi Ronchetti there are eighteen per whorl, but in fact the number increases with the size of the helicocone from not more than ten to at least twenty. Further, on the early whorls of the teleoconch each tubercle is continued abapically as a short, broad, slightly opisthocline rib running down the outer face (see Pl. 47, fig. 12).

There is no record of any comparable sculpture in C. trochlearis; indeed, Hörnes (1854:364) described his new species as having "nicht eine Spur von Spitzen oder Dornen an dem Kiele, selbst an den obersten Windungen". This is certainly true of all the larger whorls. But the British Museum specimen shows that, just as in C. calliope, the first two and a half whorls of the teleoconch bear small nodules on the carina, about twelve on the first whorl and sixteen on the next; each has a small rib beneath it. As the helicocone grows these successively diminish in relative size and eventually disappear.



FIGS. 3-7.--Protoconchs:

3. Clinura calliope (Brocchi); original drawing by D. L. F. Sealy, based on a photograph of specimen no. G. 79439 in the British Museum (Natural History).

4. *Clinura trochlearis* (M. Hörnes); original drawing by D. L. F. Sealy, based on a photograph of specimen no. GG. 2185 in the British Museum (Natural History).

5. Waitara liratula Powell; after Powell.

6. Thatcheria mirabilis Angas; after Kuroda & Habe.

7. Cryptodaphne pseudodrillia Powell; after Powell.

V. NOTES ON WAITARA LIRATULA POWELL Protoconch

Powell (1942) was the first to postulate a close affinity between Waitara and Thatcheria. He mentioned that comparative studies of the protoconchs had yet to be made; for, in any of the genera with which this work is concerned, the only protoconch known at the time was that of W. liratula described by Powell himself. Since then the protoconch of *Thatcheria mirabilis* has been described and figured by Kuroda & Habe (1954) from a beautiful specimen showing very distinct oblique reticulate ornament, and the remarkably similar protoconchs of two species of Clinura have now been described in the preceding section of the present work. If Clinura, Waitara and Thatcheria are indeed closely akin, it would be expected that the protoconchs also would be alike; this expectation is rendered even more probable by the Clinura-like tuberculation of the carina on the first few whorls of the W. liratula teleoconch, noted below. But, according to Powell (1942:169), W. *liratula* has a "dome-shaped protoconch of two whorls bearing weak protractively arcuate axial growth threads"; and his drawing (text-fig. B3 on p. 38; Text-fig. 5 in the present work) shows no ornament other than faint, slightly sinuate, slightly opisthocline striations, with no indication of others running across them. Might not this appearance have been caused by abrasion?

It was felt that the protoconch of *Waitara liratula* should be looked at again. According to Fleming (in litt.), "The paratype figured by Powell (pl. 14, fig. 8) is apparently the same specimen on which he based his text-fig. B3 . . . The holotype and other paratypes are still more deficient in protoconch. . . . We have no evidence whether the protoconch was damaged after Powell's figure was made." The figured paratype (Pl. 47, fig. 7) was therefore sent to London and examined with great care. Unfortunately the specimen does seem to have been damaged since Powell described it twenty years ago, for, whatever its condition before, the protoconch is now in such a poor state of preservation that it is difficult to compare it with Powell's drawing and impossible to see any traces of its original ornament. Indeed, the protoconch is far too worn and damaged to afford positive evidence of any significant difference between *Waitara* and *Thatcheria* in this taxonomically important character. A close relationship between *Waitara* and *Thatcheria*, as originally suggested by Powell himself, is therefore still quite possible.

Transverse sculpture

During the examination of the figured paratype of *Waitara liratula* it was noticed that the first two or three whorls of the teleoconch bore unmistakable indications of nodules on the carina, arranged with an appearance of regularity. The angular distance between consecutive nodules was estimated at about 20° of arc; thus, originally, there would have been about eighteen nodules per whorl. Beneath some of these there were traces of a short, broad and markedly opisthocline rib running down the outer face of the whorl. After the first few whorls, however, the carina became smooth. This character has not previously been recorded in *W. liratula*.

The Neogene shells from Okinawa which MacNeil (1960; see above, p. 268) described as *Thatcheria* cf. gradata seem to have a close affinity with *W. liratula*, even though it must be admitted that comparisons are difficult when they have to be made from one illustration of a single incomplete specimen of each species. The early whorls of the teleoconch of the figured specimen from Okinawa are far better preserved than in Powell's specimen and bear distinct nodules on the carina, exactly like those of *Clinura calliope*; these gradually become less distinct and eventually disappear at a point where the transverse diameter of the shell (measured across the carina) is about 4 mm.

Marwick (1931:149) reported that the early whorls of W. generosa bore about twelve low, rounded axial costae extending downwards from the keel and forming weak tubercles at their intersection with the shoulder-angle.

VI. SYSTEMATICS

General principles

The classification of the gastropods discussed in this work, except that of the Recent *Thatcheria mirabilis*, is necessarily based entirely upon their shell characters.

It has been generally believed that the most fundamental of these are the position and form of the posterior sinus, indicated in incomplete specimens by the position and form of the collabral growth-lines; this feature is considered to be the most useful of those by which a turrid may be distinguished from other Toxoglossa and assigned to a sub-family within the Turridae. But the posterior sinus is not infallibly diagnostic in these matters. In the Conidae, which are without doubt close relatives of the Turridae, the form of the posterior sinus varies not only from species to species but even within a species, and it is sometimes just like that of certain Turridae. For example, the collections of the British Museum (Natural History) include a series of shells of the Recent Conus pennaceus Born 1780, all characterised by a particular colour pattern. One of these, however, has a posterior sinus which resembles that figured by Powell (1942, text-fig. F28) as belonging to the Recent turrid Asperdaphne versivestita (Hedley 1912) [Daphnella]; another has the "reversed L " sinus more typical of the Daphnellinae (as found in Daphnella cancellata Hutton 1878); in a third specimen the sinus is similar to that of Clinura or Thatcheria; and in a fourth it is virtually absent. In other individuals it is vet again quite different from any of these. Thus there can be no such thing as a sinus typical of the Conidae, although Powell (1942:167), who mentioned the "deep Conid-like " sinus of his Thatcheriidae, clearly implied that there was. Again, Powell (p. 28) wrote of the Turridae that "Position and style of sinus is the best guide to subfamily grouping." Experience may indeed have shown that there is no better, but the guidance afforded by the posterior sinus provides no simple key to this problem; its form, if not its position, may vary widely within a given subfamily. In short, the posterior sinus appears to be of systematic value only when the taxonomic placing indicated thereby is confirmed by other distinctive characters with which it has no connexion.

It was therefore necessary to bear other characters in mind when considering whether or not the molluscs in question should be referred to the Turridae and, if so, to which particular sub-family thereof. Those characters were the nature of the protoconch and the absence of a tendency towards the resorption of the columella and early internal walls. Further, when a series of shells was thus referred to a given grouping, their possession of a common suite of less distinctive characters (such as a pagodiform spire, a certain distribution of spiral ornament, and a certain type of columella) offered additional confirmation of their relationship.

Generic and specific separation were effected primarily upon the presence or absence of transverse sculpture and tubercles, and secondarily upon a number of other characters—the position of the carina on the whorl, the degree of development and precise nature of the spiral ornament, the degree of "pagodiformity", the spire angle, and the height of the spire relative to that of the last whorl and aperture.

In living Toxoglossa the soft anatomy (where known) affords more evidence of the animal's affinities. The morphology of the radula is important in this connexion. The presence or absence of an operculum, and, when present, its structure, are also characters which are generally of taxonomic value only in Recent forms. Fossil gastropods are rarely associated with opercula, even where they are known to have possessed them, and the seeming absence of an operculum in a little-known form is thus without significance.

The Clinura-Thatcheria group

As mentioned above (p. 262), it was suggested by Beets (1943b) that Clinuropsis, Clinura and Thatcheria formed a closely related group. He regarded Cochlioconus as part of Thatcheria, and did not consider Waitara at all. But Powell (1942) had already recognised a relationship between Waitara and Thatcheria; and Wenz (1943) placed Waitara (at that time known to him only by its Miocene species) near Clinura, although he thought that Thatcheria and Cochlioconus had no affinities with either, or even with each other. Beets, therefore, in a later paper (1951), added Waitara to his group.

This suggested grouping has evoked no mention or comment elsewhere. The forms in question certainly seemed to possess some characters in common and no fundamental differences; in particular, the shell was always more or less pagodiform, with a juxtasutural posterior sinus (admittedly of variable depth) having its vertex close to the suture. All the species seemed to be extremely rare, and were probably abyssal in habit.

More conclusive evidence of this supposed relationship is now available, although the extent of the group requires limitation. Beets' conception of the taxon Clinura was a very wide one, even in the more restricted sense in which he used it in 1951. His misunderstanding of the true form of the posterior sinus in the type-species, C. calliope (Brocchi), had led him to believe that the depth of the sinus, since it appeared to vary greatly in species which were otherwise similar, was subject to " normal" variation within the group; yet, in the same work (1943b: 364), he stated that the form of the sinus was "ein Merkmal von höchster Bedeutung in der Systematik der Turridae". It has now been made quite clear (see p. 272] that the posterior sinus of the type-species is very deep; and it is also apparent (see Pl. 47, figs. 3, 6, 8, 11) that its exact shape as found in C. calliope is a constant character of Thatcheria (including Cochlioconus), of Waitara, and of certain other species referred to Clinura itself, but not of the remaining species hitherto referred to Clinura and not of *Clinuropsis*. It is therefore suggested, in accord with Powell and Beets, that the highly distinctive type of sinus found so consistently in these genera is indeed of taxonomic value, notwithstanding what has been written above concerning the variable position and form of the posterior sinus in the Toxoglossa in general. (This, of course, would not be true if a sinus like that of Thatcheria could be clearly shown to have developed as a result of parallel evolution in an entirely different group.) It is further suggested that any alleged species of *Clinura* without this deep sinus have been wrongly placed in that genus. An examination of the original descriptions and figures of most of the species mentioned by Cossmann (1896:75); Grant & Gale (1931:494); Beets (1943a:296,297;1943b:358-64); Eames (1957:51)and Glibert (1960: 25, 26) indicates that this exclusion from Clinura should apply to all the species from North America (Eocene to Miocene), Africa (Palaeocene and Eocene), and the Palaeocene and Eocene of Europe, and to most of those from the Neogene of Europe; thus it is not possible to agree with Beets that the genera Clinuropsis Vincent 1913 (non Thiele 1929) and Nekewis Stewart 1927 should be placed in the synonymy of *Clinura*. Indeed, the only true species of *Clinura* (using

the name in Beets' narrower sense, thus also excluding *Waitara*, *Cochlioconus* and *Thatcheria*) seem to be the type-species and a few others from the Neogene of Europe, together with the two species from the Neogene of Buton (Celebes).

It is noteworthy that the only species (other than C. calliope) mentioned by Bellardi when proposing the genus Clinura was C. elegantissima (Foresti 1868) [Pleurotoma], which, by the form of its growth-lines, is clearly not a Clinura. Its complex spiral ornament is also very distinctive. On the other hand, a good example of a European species accepted here as a Clinura is C. trochlearis (M. Hörnes 1854) [Pleurotoma]. In the present work, the decision to retain this species within the genus Clinura was originally based upon Hörnes' description and figures, with particular reference to the form of the posterior sinus; only later did this decision receive powerful support from the discovery that an individual of C. trochlearis in the collections of the British Museum (see p. 274) showed a diagonally cancellate protoconch, just as in C. calliope, and transverse, slightly opisthocline costae on the juvenile whorls of the teleoconch. Another species which may be assigned to Clinura with a high degree of probability is C. controversa (Bellardi 1847) [Pleurotoma]; Bellardi, incidentally, ascribed this new specific name to Jan 1845 " in litt. et specim." (p. 64).

More doubtful cases, where it would probably be difficult to make a definite decision on the correct systematic position of the species without handling the actual type-material, include *C. sopronensis* (Wolf 1870) [*Pleurotoma*], *C. subtrochlearis* (Friedberg 1912) [*Surcula*], and *C. sabatiorum* Bellardi 1878. But it is felt that a full examination of every species attributed to *Clinura* by one author or another, often without justification, is beyond the scope of the present review. The species excluded would form such a large and varied assemblage, with such a wide geographical distribution and such a long stratigraphical range, that they would doubtless represent several distinct genera. The available genera to which they might be referred would include those listed by Grant & Gale (1931) and by Beets (1943b) as synonyms of *Clinura*, other than *Thatcheria* and *Cochlioconus* : namely, *Clinuropsis* Vincent 1913 (*non* Thiele 1929) and *Nekewis* Stewart 1927. It is possible, however, that not all species might be referred to those or to other existing genera, in which case new genera would be needed.

The Butonese species of *Clinura* are *C. carinata* (Martin 1933) [*Cryptoconus*] and *C. bituminata* (Beets 1943*a*) [*Surculites*].

If the genus *Clinura* be limited as suggested above, which to me seems perfectly reasonable, then the reasons for postulating a close relationship with *Waitara* and *Thatcheria* (including *Cochlioconus*) are much more convincing. But there are no grounds for supposing these forms to be related just as closely to the genus *Clinuropsis*.

Confirmation of this affinity is given by the protoconchs. Until a few years ago that of *Waitara* was the only one described (Powell, 1942). Now, however, the protoconchs of the type-species of *Clinura* and *Thatcheria* have been made known (see p. 274 above; and Kuroda & Habe, 1954); both show the same type of diagonal reticulation, and this suggests a relationship between those two genera. On the other hand, the *Waitara* protoconch described by Powell gives no indication of

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diagonal cancellation; but, as stated above, its condition is so unsatisfactory that the nature of its original ornament cannot be ascertained. At least it affords no evidence to refute the suggestion, based on other conchological evidence, that *Waitara* is related to *Clinura* and *Thatcheria*. In any case, the species in question (*Waitara liratula*) is not the type-species of *Waitara*.

Other common characters of the shells, which might be of little taxonomic value on their own, together reinforce the evidence already cited for the relationship of the three genera. They include the pagodiform habit, the distribution of the spiral ornament on the outer surface of the teleoconch, and the smooth, very slightly twisted nature of the columella. The distribution of the spiral ornament cannot always be ascertained very easily from the published descriptions and illustrations; but the ornament is typically confined to the outer face of each whorl, except in that there are comparatively weak striations on the outer edge of the ramp (next to and parallel with the carina). This type of distribution is certainly found in *Clinura calliope*, *C. trochlearis*, *C. bituminata*, *Waitara pagodula*, *W. liratula*, and in the new species of *Thatcheria* from Fiji described below. In the Recent *Thatcheria mirabilis*, of which the material is of course in a far better state of preservation, the spiral ornament on the ramp extends further towards the adapical suture, but it is altogether fainter than in the other species and is in no way comparable with the much stronger striation of the outer face.

The value of Beets' eventual conclusion, that Clinuropsis, Clinura, Waitara and Thatcheria (including Cochlioconus) form a closely related group, may therefore be assessed as follows. His suggestion was based at the time on inadequate evidence ; but a more restricted conception of the genus *Clinura*, coupled with better understanding of the form of the posterior sinus in that genus and with new knowledge of the form of the protoconchs in *Clinura* and *Thatcheria*, now indicates that it is perfectly reasonable in so far as Clinura, Waitara and Thatcheria are concerned. Clinuropsis, however, does not form part of this group. Further, it cannot be agreed that the similarities between the three named taxa in the group are sufficiently close to justify placing them all in synonymy (senior synonym Clinura, ranked as a sub-genus of Surculites in Beets, 1943b), or even to warrant their being considered as three separate sub-genera of Surculites (in Beets, 1951). In the following argument they are regarded initially as three distinct genera. In any case, close affinity with Surculites is denied in the present work; the matter is discussed more fully below (p. 289), where the external relationships of the Clinura-Thatcheria group are considered in detail.

At present, then, this group appears to include at least the following species :

Clinura calliope	Waitara waitaraensis	Thatcheria mirabilis						
C. trochlearis	W. generosa	T. gradata						
C. controversa	W. pagodula	Thatcheria sp. nov. Beets						
C. bituminata	Waitara sp. nov. Powell	1951						
C. carinata	1942 aff. pagodula							
	W. liratula							

Division into genera

The species referred to Waitara seem, in general, to be intermediate in character between Clinura and Thatcheria. This division of the group into three genera, however, appears rather unsatisfactory : like species are separated (C. carinata and W. pagodula, W. liratula and T. mirabilis) and unlike species placed together (C. bituminata and C. carinata, W. generosa and W. liratula). A careful consideration of all the species involved has led to the following conclusions.

All three species listed as *Thatcheria* are correctly regarded as congeneric with each other. But several other species listed above (*Clinura carinata, Waitara pagodula, Waitara* sp. nov. Powell 1942 aff. *pagodula, W. liratula*) and the new species from Fiji described below as *Thatcheria vitiensis* are all very similar to the three species of *Thatcheria* listed; they resemble them in having the carina generally high on the larger whorls and only weak spiral ornament, and in being entirely free of transverse ribbing or tubercles at every stage of development (except, in three cases, for minute vestigial nodules on the very youngest whorls of the teleoconch), while they differ from them chiefly in being less pagodiform. Indeed, there is little more than the variable degree of pagodiformity to distinguish any of these eight species from each other. It is therefore suggested that they should all be placed in the genus *Thatcheria*.

The geographical distribution of the genus as thus enlarged remains entirely within the area of the Western Pacific. Its stratigraphical range extends from Upper Miocene to Recent, but it is predominantly Pliocene.

Powell (1942), of course, recognised the affinity of *Waitara* and *Thatcheria* (see pp. 260,261), "probably basing his opinion mainly on the features of two species of *Waitara* newly described by him" (Beets, 1951:16). But, because he had misinterpreted the form of the posterior sinus of *T.mirabilis* from the growth-lines shown in Angas' rather misleading figure, he doubtfully retained *Waitara* as a separate genus "for New Zealand usage". Beets (1951:16) pointed out that the sinus in *T. gradata* [*Cochlioconus*] " is almost similar to that in *Waitara*", but he failed to realise Powell's mistake in the matter of the *T. mirabilis* sinus, even though he himself had earlier figured it correctly (1943b, pl. 36, fig. 2). However, this misinterpretation has now been explained (pp. 269, 270); and Powell's younger species of *Waitara* (though not Marwick's two older species, one of which is the type-species) have been referred to *Thatcheria*.

On the other hand, if it should later transpire that the protoconch of T. *liratula* and its allies (known in only the one specimen of T. *liratula*, which seems to have been subsequently damaged) is, as appears from Powell's description and figure, essentially different from that of *Thatcheria*, then it would be necessary to erect a new genus for those forms.

If the younger species formerly ascribed to *Waitara* are transferred to *Thatcheria*, then the only species remaining in the former genus are the type-species *waitaraensis*, from the Upper Miocene of New Zealand, and *generosa*, from the Lower Miocene of the same country. Marwick's fairly detailed generic diagnosis of *Waitara* appears to be based equally upon *waitaraensis* and *generosa*, so that, as mentioned above (p. 261), Wenz (1943) was misled into believing that *generosa* was the type-species

of the genus. But, as far as can be judged from Marwick's descriptions of these two species, only one individual is known of each. The holotype of *waitaraensis* in particular is very incomplete and seems to have suffered distortion; there are no highly distinctive characters, either positive or negative. It therefore seems that the genus *Waitara*, defined objectively by reference to this single specimen, cannot be defined very clearly. It is nevertheless obvious from Marwick's descriptions and figures that, unlike *W. pagodula* and *W. liratula*, neither *W. waitaraensis* nor *W.* generosa can be referred to *Thatcheria*. Neither species is much less pagodiform than is *T. liratula* or the new Fijian species *T. vitiensis*—indeed, they are probably more pagodiform than is *T. pagodula*—but their whorls have an entirely different aspect.

On the other hand, Beets wrote (1951:16) that "there are also relationships between Waitara in its former sense (i.e., as based upon W. generosa and W. waitaraensis) and Clinura". This appears to be true at least of W. generosa, which has both the characteristic attributes of a Clinura : the first few whorls of the teleoconch are ribbed, with tubercles on the carina, and the carina is low on the larger whorls (that is, the ramp slopes steeply downwards). These show its affinity with the European species of Clinura (including the type-species, C. calliope) and with the Butonese C. bituminata. It is therefore proposed that W. generosa be transferred to the genus Clinura. As for W. waitaraensis, the incomplete and distorted nature of the specimen prevents its giving any information on these characters; but, since Marwick (who handled the material) believed it to be congeneric with W. generosa, it may also be transferred—albeit provisionally—to Clinura, thus making Waitara a subjective junior synonym of Clinura. If better material later showed that this transfer, though correct for W. generosa, was not justified in the case of W. waitaraensis, the generic name Waitara would still be available for the latter species.

The genus *Clinura*, as listed above, has now lost *C. carinata* to *Thatcheria* but has gained the species *waitaraensis* and *generosa* from *Waitara*; i.e., it includes the species *calliope*, *trochlearis*, *controversa*, *bituminata*, *generosa*, perhaps *waitaraensis*, and possibly others from Europe. The geographical distribution of the genus in this new sense is thus restricted to Europe (the Mediterranean Basin), the East Indies and New Zealand. The European species are all of Miocene age, although some (such as *C. calliope* itself) persist into the Lower Pliocene (Plaisancian); the Butonese species is of Neogene age, very probably Upper Miocene; and the two New Zealand species, as mentioned above, are from the Lower and Upper Miocene respectively. It may therefore be said that the stratigraphical range of *Clinura* is from the Lower Miocene to the Lower Pliocene, but that the genus occurs mainly in the Middle and Upper Miocene.

The stratigraphical range of *Clinura* contrasts with that of *Thatcheria*, essentially Pliocene to Recent. This shows that the most natural break in the *Clinura-Thatcheria* group occurs between the earlier and the later species of "*Waitara*" at about the level of the Miocene-Pliocene boundary. It seems, however, that there is a certain amount of overlap on either side of that boundary. In one direction *C. calliope* survives into the Plaisancian, as do other possible species of the genus (see Glibert, 1960: 25, 26); in the other, rocks which are probably no younger than

Upper Miocene already contain *T. carinata*, and *T. pagodula* may likewise be of Upper Miocene age.

The genus *Clinura*, even in the restricted sense used here, cannot be defined very easily; it is essentially a rather variable assemblage of species, of wide distribution and of predominantly Miocene age. *Thatcheria*, on the other hand, even in the present broad interpretation, is a fairly homogeneous group of species and may be defined quite clearly. It seems that it originated from *Clinura* towards the end of the Miocene, became widespread in the Western Pacific area during the Pliocene, and survives to the present day as the one rather "extreme" form living in deep waters off the Japanese coast.

T. mirabilis may in fact occur more widely than is known at present, "off Japan"; for a rare abyssal form is far more likely to be recovered in the Kii region, off the south coasts of Honshu and Shikoku, than anywhere else in the Pacific. Not only is the Pacific Ocean almost at its deepest off Japan, but in few places are there such deep waters so near to a large area of land. Indeed, they are nowhere else so close to a heavily populated shore-line from which intensive fishing is carried out.

Interspecific differentiation in Thatcheria

The eight species referred in this work to the genus *Thatcheria* seem to differ from each other in little more than in certain characters of the spire : in its degree of pagodiformity, in its acuteness, and in its size relative to that of the last whorl and the aperture. In general, the various species seem to form an evolutionary series in which the degree of pagodiformity increases with time ; and, as it increases, the spire appears less acute.

It is very difficult, if not impossible, to define "pagodiformity" objectively. Several numerical properties of pagodiform shells were examined as possible indices but rejected for various reasons; they are shown in Text-fig. 8. Measurement of the spire angle proved more useful, for this, in a shell of the type under consideration, can be measured in two different ways (Text-fig. 9). The term "internal spire angle" may be introduced for the angle between the two lines which, on either side of the spire, connect the intersections of the suture with the lateral profile. It is obvious that only an approximate value can be obtained for this, for the lines are unlikely to be straight; it is not even likely that smooth continuous curves can be drawn to pass exactly through all the points, and the best that can be obtained will nearly always be a slightly concave curve passing close to most of them. The "external spire angle" is measured in a similar manner but is based on the intersections of the carina with the lateral profile ; it is, of course, larger than the internal spire angle.

Of the eight species of *Thatcheria* in which such measurements were possible (including *T. vitiensis* sp. nov. described below), seven gave a value for the internal spire angle which was remarkably constant, lying always between 38° and 46° ; exact measurements would not be especially significant, for, even in different individuals of one species (the Recent *T. mirabilis*), the angle varied between 38° and 44° . Only *T. pagodula* gave a significantly different value, 57° .

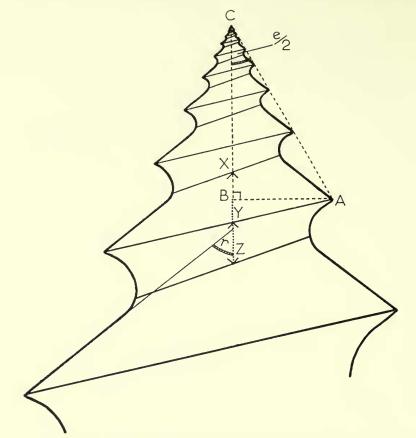


FIG. 8.—Plane projection of the spire of an idealised pagodiform shell, to illustrate the numerical properties examined as possible indices of pagodiformity but rejected for various reasons. They are :

(a) The projection of the carina, expressed as the ratio of its perpendicular distance from the shell axis (AB) to the distance of that perpendicular from the apex (BC). This is the tangent of half the external spire angle (e).

(b) The angle (r) between the profile of the ramp and the shell axis.

(c) The height of the carina on the whorl, expressed as the ratio of its axial distance from the lower suture (YZ) to the axial distance between the sutures (XZ).

On the other hand, the external spire angle varied greatly, from 50° in the earliest species *T. carinata* to 82° in the holotype of the Recent *T. mirabilis*. It seemed to show a fairly steady increase with the passage of time; but *T. pagodula* was once again the exception, with an external spire angle of 71° . This higher value, however, is consistent with the higher value for the internal spire angle. In fact, the ratio of the external spire angle to the internal, which might be called the "index of pagodiformity", is the same in *T. pagodula* as in the much slimmer *T. carinata* (the only other species of possibly Miocene age)—namely, 1.25.

To sum up, then, the situation seems to be that there are two species of *Thatcheria* of possibly Miocene age. One of these (T. carinata) has an internal spire angle of

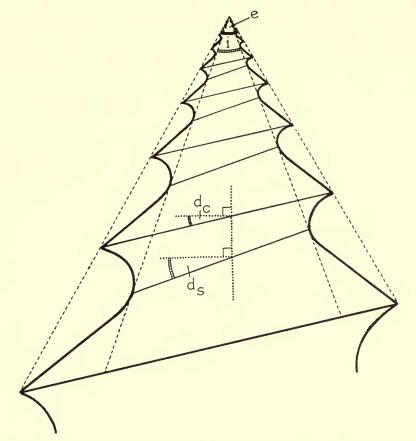


FIG. 9.—Plane projection of the spire of an idealised pagodiform shell, to illustrate : i—the internal spire angle,

e-the external spire angle,

 d_s —the angle of declination of the suture, and

 d_c —the angle of declination of the carina.

Note :

(a) d_s is greater than d_o in a pagodiform shell, for the suture descends in a tighter (and therefore steeper) spiral than does the carina.

(b) Both d_c and d_s are smaller than they appear in the plane projection. This is because, in the plane projection, both carina and suture appear to descend from one side of the shell to the other in a straight line; whereas, in fact, they do so on the surface of a cone and therefore less steeply.

$$(c)\frac{\tan d_s}{\tan d_c}$$
 should be equal to $\frac{\tan e/2}{\tan i/2}$.

40°, the other (*T. pagodula*) has a much broader spire (internal spire angle 57°); but both have exactly the same index of pagodiformity (1.25). All the later species have an internal spire angle which is much the same as in *T. carinata*; but the index of pagodiformity, like the external spire angle, shows an increase with the passage of time—to 1.50 in the two supposed Lower Pliocene species (*T. liratula*, *T. vitiensis*), to 1.58–1.62 in the two species described simply as "Pliocene" (*T.*

gradata, Thatcheria sp. nov. Beets 1951), and to 1.75-2.05 in the Recent T. mirabilis.

It seems likely that the index of pagodiformity will prove to be more constant and characteristic for a given species than either the internal or external spire angle; for the two spire angles, though they may vary considerably between individuals, seem to do so together. Use of the index, though liable to considerable error, may afford a rough indication of the course of evolution.

Of course, the position of a species on the evolutionary scale (and hence its approximate geological age) should not be assessed on any one character alone. The various characters probably evolved at different rates in different lineages.

Evolution in the Clinura-Thatcheria group

Clinura calliope, type-species of the genus *Clinura*, ranged from Upper Miocene to Lower Pliocene. *Clinura*, however, was already well diversified at the beginning of that time; thus the type-species occurred too late to occupy any central position in the phylogeny of the genus as defined in the present work. Moreover, in one prominent feature *C. calliope* differs from the other species which are considered here to constitute that genus: the entire carina is furnished with well developed tubercles.

A better claim to a central position may be made on behalf of *C. trochlearis* (from the Middle Miocene¹ of Europe). Unlike every other species referred to *Clinura*, *C. trochlearis* may be placed in that genus with absolute certainty. Except for the poorly known, rather peculiar *C. generosa* in the Lower Miocene, it is probably the oldest species of *Clinura*. It is somewhat variable in form, especially with regard to the acuteness of the spire and the position of the carina on the whorl. And it is also the most "central" in form; for it could well be ancestral, by a late Miocene radiation, to all the Upper Miocene species of *Clinura* and to *Thatcheria*.

Of those species in the Upper Miocene, C. waitaraensis is rather like C. bituminata in the general aspect of its whorls, which, where undamaged, seem to have a steeply inclined ramp and a low carina; further, both those species are very similar to C. trochlearis. C. bituminata and C. waitaraensis could be derived from a common ancestor which, in turn, had evolved from C. trochlearis with little change in form. Migration from Europe to the south-western Pacific would have occurred at the onset of this hypothetical evolution.

Another species in the Upper Miocene of the south-western Pacific which also is similar to *Clinura trochlearis* is *Thatcheria carinata*; the flatter ramp and higher carina distinguish it from *C. bituminata* and *C. waitaraensis*. Like those two species, *T. carinata* may have been derived from a migrating descendant of *Clinura trochlearis*. From *Thatcheria carinata* a line of evolution to the Recent *T. mirabilis* may be envisaged; it has been shown above that, with passage of time, the internal spire angle remained more or less constant while the external spire angle (and hence the index of pagodiformity) gradually increased. Only *T. pagodula*, with its generally much stouter spire, would necessarily have formed a distinct Upper Miocene offshoot from this series. It also seems that the evolution of *Thatcheria* from

¹ Some authorities now prefer to regard the Zweite Mediterran-Stufe (Suess, 1866) of the Vienna Basin as Tortonian in age, i.e. Upper Miocene, rather than Helvetian. But *C. trochlearis* occurs also in the Middle Miocene of Italy (Bellardi, 1877: 206).

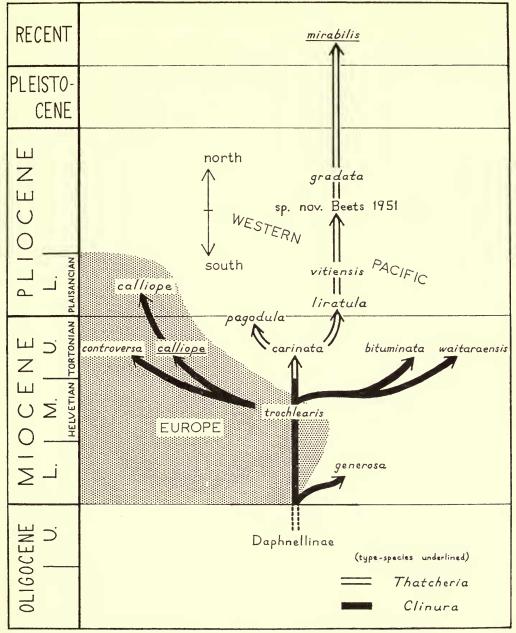


FIG. 10.—A very tentative evolutionary tree of the Thatcheriinae.

the Miocene onwards has been accompanied by a northward movement of the population towards its present home in the north-western Pacific.

The only other species in the Upper Miocene which have definitely been referred to *Clinura* are both from the Mediterranean region, *C. calliope* (the type-species, persisting into the Lower Pliocene) and *C. controversa*. A list of characters distinguish-

ing these two species (at that time referred to *Pleurotoma*) was drawn up by Bellardi (1847:64); in fact, it was largely by means of this comparison with *P. calliope* that he described his new species *P. controversa*. Once again *C. trochlearis* may be regarded as a possible ancestor—of *C. calliope*, *C. controversa*, or both,—but in this case there is no need to postulate a distant migration of the stock. The tendency towards the development of transverse sculpture on the first few whorls of the teleoconch, manifested in *C. trochlearis* and in other early species of the group, might have led to the evolution of *C. calliope* by affecting the whole shell; and, in similar fashion, *C. controversa* might have evolved through the development of a notched carina.

As for *Clinura generosa* in the Lower Miocene, this species has a somewhat different appearance; it is difficult to imagine it as a direct ancestor of *C. trochlearis* and of all the other species mentioned. But it has the typical posterior sinus of the *Clinura-Thatcheria* group, together with the tubercles on the early whorls of the teleoconch. It must therefore be retained within the group, in the genus *Clinura*, and placed on a sterile side-branch of the evolutionary tree.

All these suggestions are summarised in Text-fig. 10.

Systematic position of the Clinura-Thatcheria group

Serious consideration of *Thatcheria* and its relatives has led most modern authors to place them in the Turridae (Eales, 1938; Beets, 1943b, 1951; Kuroda & Habe, 1954, implicitly; Habe, 1955). There have been only two important exceptions. Yokoyama (1928, 1930), though he did not explicitly refer *Thatcheria* [Cochlioconus] to the Conidae, thought it had affinities therewith; while Powell (1942) regarded *Waitara*, Cochlioconus and Thatcheria as constituting a new family, the Thatcheridae, distinct from the Turridae (though parallel to them) and more closely related to the Conidae.

Preference is given here to the view that this group of gastropods is best placed in the Turridae. The posterior sinuses of *Clinura* and *Thatcheria* may indeed be compared with those of certain Conidae (e.g., *Conus araneosus* Solander 1768); although, in general, the outer lip is drawn further forward in *Clinura* and *Thatcheria* before it crosses the line of the carina. On the other hand, their posterior sinuses also resemble those of certain turrids; the diagonally cancellate ornament on the protoconchs of *Clinura* and *Thatcheria* is a turrid character; and neither genus is known to show any manifestation of the tendency, typical of the Conidae, to resorb the columella and early internal walls. Further, the form of the radula in *Thatcheria mirabilis* and other characters of that Recent species confirm the opinion that the group should be referred to the Turridae, particular significance being attached to Eales' work upon the soft anatomy. There would seem to be little or no justification for the erection of a separate family to accommodate *Clinura* and *Thatcheria*, even if that family should be considered as having turrid rather than conid affinities.

Clinura, of course, had been placed in the Turridae (Pleurotomidae) from the very date of its establishment in 1875, long before Eales (1938) wrote her paper on *Thatcheria* and long before it was first suggested that the two genera were related. A brief history of the more exact classification of *Clinura* has already been given above (pp. 263–268); sufficient here to note that, of recent years (since 1931), the taxon has

been generally regarded as a sub-genus of *Surculites*. Grant & Gale wrote (1931: 494):

"Clinura is closely related to Turricula, and might be considered a variational extreme in the opposite direction from Pleurofusia. It can, however, be distinguished generically by its shorter form and broad, shallow notch. It is even more closely related to Surculites proper, Pseudotoma, and Megasurcula, sharing with them the broad conical shape and wide shallow notch, so that it is here not separated from them generically. . . . It probably was derived from Turricula, perhaps indirectly, and later gave rise to, or is a branch of the stock that gave rise to, Pseudotoma and Megasurcula. The intergradations between it and the last named are evident in the California and Washington Tertiary. Clinura and typical Surculites are both well represented in the Eocene of the Pacific coast, . . . Clinura lived on into the Miocene, where it is represented by [Megasurcula] keepi (Arnold), . . . " It is clear from this, however, that Grant & Gale were basing their arguments largely upon the characters of the species in the Eocene of North America which they had referred to Clinura; and those species, as pointed out above, do not possess the deep posterior sinus which is considered here to be the most essential character of the genus. Their opinions, therefore, do not apply to Clinura in its proper sense.

But, in any case, Wrigley (1939: 282, 283) recognised quite correctly that the genus *Surculites* was not a turrid, having no true sinus or notch like that of the typical members of the family. He concluded that "The sinuous growth lines [of *Surculites*] here considered are not an unequivocal mark of the Turridae, they may occur in other families, linked with and proportionate to whorl-carination. *Surculites* is long extinct, we have no guidance from the animal anatomy and, in the light of the foregoing comparisons, it seems best to place the genus in a not too determinate position between the Fusinidae and the Buccinidae . . . " On the other hand, he also noted that "*Surculites* has some resemblance, especially in general form, to *Clinura* Bellardi, but in that genus the growth lines sweep back over the rear slope four or five times as far as those of *Surculites*, here showing a Turrid character, or rather, a contour often seen in the Conidae." Thus, if the species properly referred to *Clinura* have no affinity with *Surculites*, then *Clinura* cannot be regarded as a subgenus of *Surculites* (in which classification Grant & Gale (1931) were followed by Beets (1943*a*, 1943*b*, 1951).

The true characters of *Clinura* and *Thatcheria* not only link those genera with the Turridae but with a particular sub-family thereof, the Daphnellinae. Of all the turrid sub-families listed by Powell (1942:29), only the Daphnellinae have (sometimes) a diagonally cancellate protoconch (see Text-fig. 7); only the Daphnellinae possess a juxtasutural posterior sinus; only the Daphnellinae and the Mangeliinae, together with a few genera in other sub-families, lack an operculum; and the radula of the Daphnellinae, which has marginal teeth only, is very similar to that of *Thatcheria*. Indeed, Kuroda & Habe wrote of *Thatcheria mirabilis* (1954:81) that the protoconch "shows the obliquely reticulated texture of sculpture, suggesting that it is also of a Daphnelloid", and (p. 80) that the species has a radula, "whose

peculiar shape shows that it has a close affinity with the Daphnellinae".

But Powell (1942:167) had two objections to the location of *Thatcheria* and its allies in the Daphnellinae, "the lack of a typical Daphnellid apex . . . and the actual form of the sinus". It has already been shown that the only *Thatcheria* protoconch known at that time, that of *T. liratula* [*Waitara*], was so badly abraded as to be useless; but Powell was correct in supposing that the form of the *Thatcheria* sinus (either as he wrongly believed it to be in *T. mirabilis*, having been misled by Sowerby's figure to Angas' description, or as he actually observed it in *T. liratula*) was not quite like that of the Daphnellinae. The other differences between the Daphnellinae on the one hand and *Clinura* and *Thatcheria* on the other (listed below in Table II) cannot preclude the possibility that the *Clinura-Thatcheria* group originated from the Daphnellinae in the Upper Oligocene or Lower Miocene by the development of a larger, pagodiform shell; even the protoconchs of *Clinura* and *Thatcheria*, now known from one good specimen of each of three species (*C. calliope*, *C. trochlearis*, *T. mirabilis*), agree with such a theory. But, from the taxonomic viewpoint, the consistent difference between the groups in the form of the

TABLE II

	Daphnellinae	Clinura and Thatcheria
Form of posterior sinus (juxtasutural)	Typically a '' reversed L '' $\ $.	Smoothly arcuate, with outer lip drawn far forward
Protoconch (see Text-figs.	Generally diagonally cancel	Diagonally cancellate (where
3-7)	late; but never exactly like that of <i>Clinura</i> and <i>Thatcheria</i>	adequately known)
Spire	Rarely pagodiform, if ever .	Always more or less pagodi- form
Whole shell	Generally small .	Always fairly large
Earliest known occurrence .	Oligocene, perhaps even Cre taceous	Lower Miocene
Present trend	Still increasing .	Seemingly tending towards extinction

posterior sinus is more fundamental. All things considered, it seems that, while *Clinura* and *Thatcheria* should be placed in the Turridae and may well have evolved from the Daphnellinae, they form a group which is so distinctive that it is best not to regard it as part of the Daphnellinae.

The only logical alternative is to erect for them a special sub-family within the Turridae, the Thatcheriinae; i.e., it is proposed that the family Thatcheriidae Powell should be reduced in rank and the name of the taxon amended accordingly. The Thatcheriinae have a particularly close relationship with the Daphnellinae. The pagodiform habit, so characteristic of the former sub-family (especially its later members), has been evolved in a very similar manner in other sub-families of the Turridae, e.g. in the Cochlespirinae (compare *Leucosyrinx (Aforia) circinata minatoensis* Otuka 1949, pl. 13, fig. 11, from the Pliocene of Japan); but the Thatcheriinae may be easily distinguished from such parallel developments by the form of the posterior sinus.

Formal classification Family TURRIDAE

Sub-family THATCHERIINAE Powell 1942 nom. transl. herein

Shell generally fairly large. Spire short relative to size of last whorl, very slightly coeloconoid, more or less pagodiform with deep suture and well developed carina. Posterior sinus on ramp of last whorl, juxtasutural, rounded, with vertex close to suture and deepened by forward extension of outer lip; outer lip simple and slightly convex between carina and anterior canal; distinct collabral growth-lines developed accordingly on ramp and outer face of whole teleoconch. Protoconch diagonally cancellate. Spiral ornament on outer face of teleoconch, and usually on outer edge of ramp next to carina; transverse sculpture may be present on juvenile whorls of teleoconch (sometimes also on adult whorls), generally leading to formation of tubercles or notches on carina, but, alternatively, it may be entirely absent. Columella smooth, very slightly twisted. Operculum unknown and probably absent; soft anatomy of the only Recent species typically turrid; radula of that species like that of the Daphnellinae, with one pair of marginal teeth and no others.

OCCURRENCE. Lower Miocene to Recent; Mediterranean Basin and Western Pacific.

Genus CLINURA Bellardi 1875

?[1931. Waitara Marwick, p. 149.]

DIAGNOSIS. Spire slightly or moderately pagodiform with carina generally nearer to abapical suture; juvenile whorls of teleoconch (sometimes also adult whorls) bear transverse sculpture, generally leading to formation of tubercles or notches on carina; spiral ornament usually well developed.

TYPE-SPECIES. *Murex calliope* Brocchi 1814 by subsequent designation of Bellardi, 1877. Upper Miocene to Lower Pliocene; Italy and Southern France.

RANGE. Lower Miocene to Lower Pliocene (mainly Middle and Upper Miocene); Europe, East Indies, New Zealand.

REFERRED SPECIES. C. generosa (Marwick 1931) [Waitara]; Lower Miocene, New Zealand.

C. trochlearis (M. Hörnes 1854) [Pleurotoma]; Middle Miocene, Vienna Basin and Italy.

C. controversa (Bellardi 1847) [Pleurotoma]; Upper Miocene, Italy.

C. bituminata (Beets 1943) [Surculites]; Upper Miocene, Buton (Celebes).

SPECIES REFERRED PROVISIONALLY. C. waitaraensis (Marwick 1926) [Turricula]; Upper Miocene, New Zealand. (May still represent distinct genus Waitara Marwick 1931.)

[*Clinura* may also include :

C. sopronensis (Wolf 1870) [Pleurotoma]; Upper Miocene, Vienna Basin.

C. subtrochlearis (Friedberg 1912) [Surcula]; Upper Miocene, Poland,

C. sabatiorum Bellardi 1877; Lower Pliocene, Italy.

Other species from the Miocene and Lower Pliocene of Europe.]

Genus THATCHERIA Angas 1877

1928. Cochlioconus Yokoyama, p. 338.

DIAGNOSIS. Spire moderately to extremely pagodiform, with carina generally nearer to adapical suture; no transverse ribbing, no tubercles or notches on carina (except for minute nodules on apical whorls of teleoconch in earlier forms); spiral ornament usually weak.

TYPE-SPECIES. Thatcheria mirabilis Angas 1877 by monotypy. Recent; off Japan.

RANGE. Upper Miocene to Recent (mainly Pliocene); Western Pacific (New Zealand, Fiji, East Indies, Japan).

REFERRED SPECIES. T. carinata (Martin 1933) [Cryptoconus]; Upper Miocene, Buton (Celebes).

T. pagodula (Powell 1942) [Waitara]; Upper Miocene or Lower Pliocene, New Zealand.

Thatcheria sp. nov. aff. pagodula (Powell 1942) [Waitara]; Lower Pliocene, New Zealand.

T. liratula (Powell 1942) [Waitara]; Lower Pliocene, New Zealand.

T. vitiensis sp. nov. (see below) ; Lower Pliocene, Fiji.

Thatcheria sp. nov. Beets 1951; Pliocene, East Borneo.

T. gradata (Yokoyama 1928) [Cochlioconus]; Pliocene, Japan.

T. cf. gradata (Yokoyama 1928) MacNeil 1960; Pliocene (and Upper Miocene?), Okinawa.

VII. A NEW SPECIES OF THATCHERIA FROM THE PLIOCENE OF FIJI

Thatcheria vitiensis sp. nov.

Pl. 47, figs. 4-6

DERIVATION OF NAME. Viti-the Fijian name for Fiji.

DIAGNOSIS. A species of *Thatcheria* with a fairly thick shell, a relatively long and slender spire and a moderately projecting carina. The whorls bear dense, distinct spiral ornament on the outer face and a few weaker spiral striations on the outer part of the ramp. The first few whorls of the teleoconch bear minute nodules on the carina.

HOLOTYPE. The unique specimen, Brit. Mus. (Nat. Hist.) Palaeont. Dept. no. G. 91124 (collector's field number VL.1); it lacks the extreme apex of the spire, the outer lip and the anterior canal.

OCCURRENCE. In tuffaceous marls of the Vanua Levu Formation, of probable Lower Pliocene age. On the new south coast road near Savusavu, Eastern Vanua Levu, Fiji; a large breast-cut 4 miles east of Salt Lake point where the road crosses higher ground north of Naweni.

DESCRIPTION.

[Note. (1) The protoconch is entirely lacking, and the condition of the early whorls is poor. (2) Although the whole of the outer lip has been broken off, the ramp of the last whorl is preserved up to its end. Had it extended further, it

would surely have left some indication of its attachment to the outer face; and, in any case, the end of the suture is coincident with the adapical end of the last striation marking the limit of growth of the inner part of the mantle. (3) The abapical end of the shell is also missing, but may be reconstructed with a fair degree of probability by reference to T. mirabilis. (4) The surface of the shell is abraded, but only very slightly.]

Μ	EASUREMENTS.										
	Length as preserved .			•							45 mm.
	Estimated total length .										51 mm.
	Height of spire as preserved										22 mm.
	Estimated total height of sp	ire									23 mm.
	Estimated height of last who	orl					•				34 mm.
	Maximum diameter (from en	nd o	of ca	rina t	o poir	it diai	metric	ally o	opposi	te	
	on carina of last whorl)										26 mm.
	Internal spire angle .										38°
	External spire angle .					•					57°
	Angle of declination of sutu	ıre	(fror	n plar	e per	pendic	cular :	to she	ell axi	s)	
	(see Text-fig. 9)										I4°
	Angle of declination of carin	ia (s	ee T	ext-fig	(, 9)						8°

This species shows a less extreme development of the characteristic form of the type-species (T. mirabilis). The shell is rather thick and solid; this applies especially to the carina, the outer part of the ramp adjacent thereto, the columella, and the outer lip in the region of the anterior canal. The internal spire angle is a little less than in other species of the genus, the external spire angle much less than in any other species except the Miocene T. carinata; the index of pagodiformity is greater than in T. carinata or the much stouter T. pagodula, about the same as in the slightly stouter T. liratula, and less than in the other species. The height of the spire is about 80% of the estimated height of the aperture; the corresponding figure for T. liratula is about 50% (fide Powell) and for T. mirabilis 57%.

The whorl profile shows that the carina projects rather acutely; in the younger whorls both the outer face and the ramp are appreciably concave, the outer face being directed steeply downwards. On the penultimate and last whorls, however, the outer face shows a more or less straight profile; and the ramp of the last whorl has a very marked angular concavity, the angle lying rather nearer to the suture than to the carina.

The spiral ornament is very much like that of T. *liratula* and is clearly shown in Plate 47, figs. 4–6; the striations pass further into the interior of the last whorl, beyond the inner lip, than they do in T. *mirabilis*. There are very faint indications of minute nodules on the carina of the earliest whorls, just as in T. *liratula*. The growth-lines are also like those of T. *liratula*, the parts on the ramp showing that the characteristic posterior sinus of the Thatcheriinae was present; the parts on the outer face, however, are inclined much less obliquely to the shell axis than they are in the New Zealand species. One peculiarity of the holotype, if not of the species, is the series of undulating striations on the inner lip which mark the limit of growth of the inner part of the mantle.

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REMARKS. This species is closely related to *Thatcheria liratula* (Powell), to which it has an especial resemblance in its degree of pagodiformity, in the type and distribution of the spiral ornament, and in the presence of minute nodules on the first few whorls of the teleoconch. It may be distinguished from *T. liratula*, however, by its more acute spire, which is much longer relative to the aperture; by the less oblique growth-lines on the outer face; and by the fact that its carina is rather more acute, with the result that both the ramp and the outer face of each whorl generally appear a little more concave.

T. liratula is from the Opoitian (Lower Pliocene) of New Zealand. The resemblance of T. vitiensis to T. liratula rather than to any other species tends to confirm the suspected Lower Pliocene age of the marks from which T. vitiensis was collected.

T. vitiensis is also like the Okinawan form which MacNeil (1960) described as T. cf. gradata, and which, as pointed out above, seems to have a close affinity with T. liratula. The Okinawan shell, however, differs from the Fijian species in certain details. The carina appears to be rather higher on the whorl and to project further, producing an almost flat ramp and a more pagodiform spire (just as in T. gradata itself, from Japan); while the nodules on the carina of the early whorls of the teleoconch, if not better developed, are at least much better preserved than in T. vitiensis.

Associated FAUNA. Four other shells (three gastropods and one lamellibranch) were found in the Vanua Levu Formation with *Thatcheria vitiensis*. They will be described elsewhere.

VIII. ACKNOWLEDGMENTS

The specimen described above as the holotype of *Thatcheria vitiensis* sp. nov. was collected by Mr. R. W. Bartholomew of the Fiji Geological Survey Department, and was sent to London for examination by permission of Dr. N. J. Guest, Chief Geologist. Their interest and encouragement are gratefully acknowledged.

My especial gratitude is due to Dr. L. R. Cox, F.R.S., for all the help he so patiently gave me. Among the many others who kindly offered useful information, suggestions and criticism were Dr. C. Beets, Mr. S. P. Dance, Dr. N. B. Eales, Mr. C. Matheson, Prof. J. E. Morton, Mr. C. P. Nuttall, Dr. A. W. B. Powell, Mr. E. P. Smith, Mr. F. M. Wonnacott, and, in particular, Mr. D. L. F. Sealy.

Dr. C. A. Fleming, Chief Palaeontologist to the New Zealand Geological Survey, allowed me to borrow the figured paratype of *Waitara liratula* Powell.

Thanks are also due to Dr. G. Archey, Director of the Auckland Institute and Museum, for permission to reproduce Powell's text-figures of the protoconchs of *Waitara liratula* and *Cryptodaphne pseudodrillia*; to Drs. T. Kuroda and T. Habe, of Kyoto University, for permission to reproduce their text-figure of the protoconch of *Thatcheria mirabilis*; to Mr. D. L. F. Sealy, who copied those text-figures and made the original drawings of the protoconchs of *Clinura calliope* and *C. trochlearis*; and to Mr. N. P. G. Tanti, who took some of the photographs.

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